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Cover illustration: *Strymon melinus* Hübner, the common hairstreak, is one of the most widespread lycaenid butterflies in the United States. Original drawing by Callie Mack, Natural Science Illustration, 8529 Jackie Drive, San Diego, California 92119.

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GENITALIC RECASTING OF *POANES* AND *PARATRYTONE* (HESPERIIDAE)

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ABSTRACT. Hesperine skipper genera in stable use in the United States and Canada at least since 1955 are gaining "authority through repetition." But critical comparison of genitalia shows that many of those genera are grossly misdefined and polyphyletic. Problems usually extend into the neotropics. On the basis of male and female genitalic characters (and about 200 KOH-treated dissections), I precisely redefine both *Paratrytone* Godman, which is high montane in much of the central and southern Rocky Mountains of the U.S. but especially in Mexico, and a compact group comprising the "terrestrial species" of *Poanes* Scudder (as opposed to the "marsh dwellers"), which range from southern eastern and central Canada, and from California and the central Rocky Mountain region of the U.S., to northern South America (Colombia, Venezuela, and Ecuador). Two-thirds (eight) of the species currently in *Paratrytone* (including *melane* [Edwards]) go elsewhere—mostly to *Poanes*; but *Paratrytone* gets *snowi* (Edwards) from *Ochlodes* Scudder. *Poanes* also gets *macneilli* **new species** from the Sierra Nevada de Santa Marta in northern Colombia but loses two Mexican and Central American species. The fuller treatment given *Poanes* includes capsule geographic distributions of its species and discussion of male genitalia at the specific level. *Poanes zabulon* (Boisduval & Le Conte) and *Poanes taxiles* (Edwards) are unquestionably distinct species. **New combinations:** *Poanes niveolimbus* (Mabille), *Poanes monticola* (Godman), *Poanes capta* (Miller & Miller), *Poanes ulphila* (Plötz); *Paratrytone snowi* (Edwards); *Ochlodes batesi* (Bell). **New synonymies:** *Poanes taxiles* (Edwards) = *P. psaumis* (Godman); *Poanes monticola* (Godman) = *P. capta* (Miller & Miller). **Incertae sedis** (temporary floaters): *rolla* (Mabille) and *benito* Freeman ex *Poanes*; *argentea* (Weeks) and *barroni* Evans ex *Paratrytone*.

Additional key words: genitalia (male and female), taxonomy, nearctic, neotropical, *Ochlodes*.

Our butterflies are supposed to be taxonomically well-known. Consider our skippers: half the nearly 300 species recorded from the United States are hesperiines, and their generic placement has not changed since the American hesperiine volume of Evans (1955). With the flood of North American butterfly books and checklists in recent decades, these stable skipper genera are gaining what I call "authority through repetition." In fact, much is generically wrong.

If critically studied and compared, genitalia are as valuable for group-

ing related species in higher categories like genera as they are for distinguishing species. Over the past six years, I have been genitally reviewing (in both sexes) much of the nearctic hesperiine fauna—and some of its neotropical connections—with an eye to better defining our “familiar” genera.

Major errors reported so far—involving *Atalopedes* and *Hesperia* (Burns 1987, 1989), *Amblyscirtes* and some of its relatives (Burns 1990), and *Atrytone* and *Mellana* (Burns unpubl.)—are the tip of a taxonomic iceberg. There are so many hidden mistakes that I need a faster way of addressing them. Some quick remedies will, of necessity, be partial or transitional. But dispatch is desirable because faulty classification continues to distort information in our new butterfly books, making broader biological generalizations and comparisons meaningless.

This paper is an effort to recast *Poanes* and *Paratrytone*—two sizable polyphyletic genera that include nearctic species—without going into needless detail. Since the primary problem at this stage is bringing related species together while dismissing the rest, problems at and around the species level (which have always intrigued me), and analyses of phylogeny, get short shrift. Traditional butterfly characters of wing color and pattern are dispensable, owing especially to rampant parallelism and convergence; but characters of the genitalia are crucial. I am resurrecting eleven genitalic illustrations from the turn of the century and the mid-twenties both to acknowledge pioneer workers whose forgotten figures still convey what we need to know (Godman 1900, Skinner & Williams 1924a, 1924b) and to save time (new and better genitalic figures would be long in coming).

A PART FROM *POANES* SCUDDER

I am actually concerned here with a subgroup of what now passes as *Poanes*, to wit, the “ordinary terrestrial species” such as *hobomok* (Harris), *zabulon* (Boisduval & Le Conte), and *taxiles* (Edwards), as opposed to the four specialized “marsh dwellers,” *massasoit* (Scudder), *viator* (Edwards), *aaroni* (Skinner), and *yehl* (Skinner). Though all are related, I cannot yet say whether the peculiar *massasoit*—the type species of *Poanes*—is truly congeneric with the terrestrial species (or even, for that matter, with the other marsh dwellers). My continued application of the generic name *Poanes* to the terrestrial species is conservative and provisional.

With flamboyant asymmetric titillators augmenting the penis of the male and correspondingly and indescribably elaborate wrinkles complicating the copulatory duct of the female, the genitalia in the terrestrial species of *Poanes* are collectively odd; but, at the same time,

they are interspecifically similar. In other words, the species are minor variations on a major theme.

In defining this theme—this genitally compact group—I have extracted shared critical features from a total of 75 KOH-treated genitalic dissections (45 males, 30 females) of all included species. My working description of each sex has been read against each of the individual dissections in order to polish it and to better accommodate variation.

Many additional genitalia have been examined and compared in connection with the grander setting, which involves (among other things) the marsh dwellers, some Asian kin, and certain skippers now in *Poanes* that cannot possibly belong. Specifically, *rolla* (Mabille) from Costa Rica and Panama and the much more recently described *benito* Freeman from southern Mexico superficially resemble *Poanes* without being anywhere near it. Together, they are going to another genus (Burns unpubl.).

The terrestrial species of *Poanes* range from southern eastern and central Canada, and from California and the central Rocky Mountain region of the United States, to northern South America (Colombia, Venezuela, and Ecuador).

Male Genitalia

(Figs. 1–16)

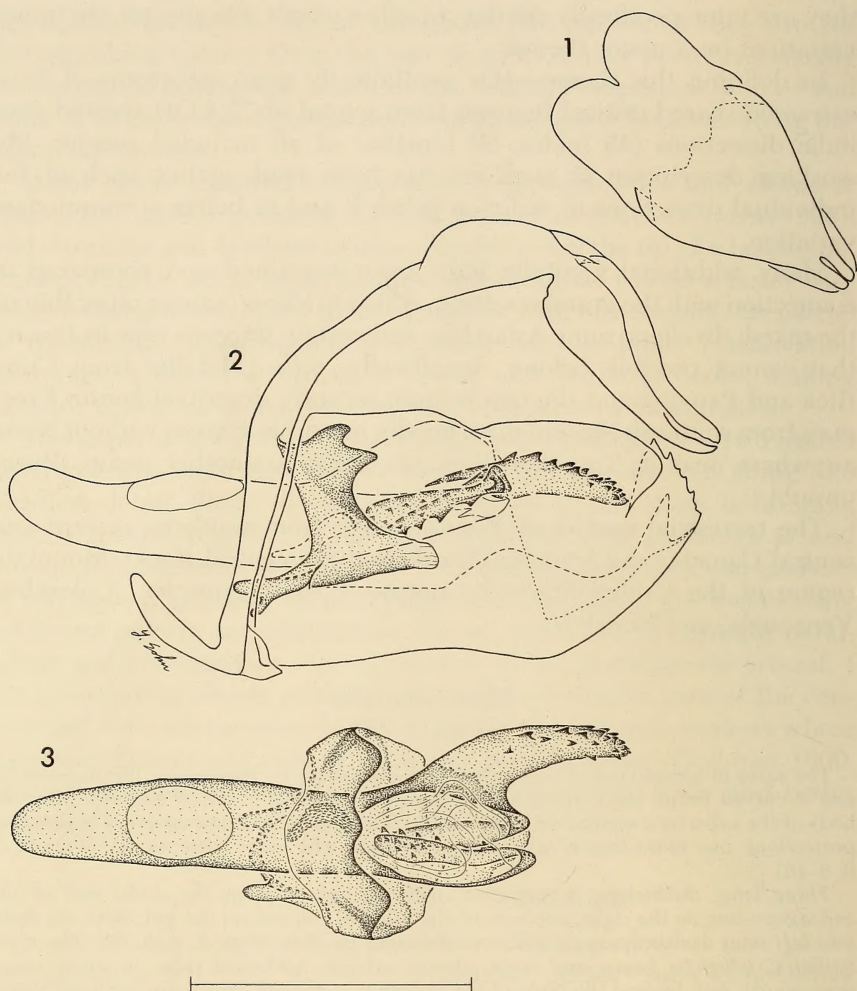
The valva in lateral view is longer than high and basically rectangular, but its posterior end is curved rather than straight. *This curved distal end is set off dorsally from the body of the valva by a vertical slit or notch and is itself divided into two dorsally-pointing projections, one more lateral (and always dentate), the other more medial* (Figs. 2, 5, 6, 8–16).

Three long, distinctive, asymmetric titillators sprout from the distal end of the aedeagus—one on the right, one toward the middle, and one on the left. Both the right and left ones are conspicuous and conspicuously dentate (Figs. 2, 3, 5–16). *The right titillator, which is heavy and rigid, always extends backward* (also, in many cases, downward), well beyond the body of the aedeagus. Although the central titillator shares an origin with the right one (Figs. 3, 6, 7), it approaches the left one; and, together, *the central and the left titillators, which are much more delicate than the right, fold on themselves 180° to run forward inside the aedeagus* (see especially Fig. 3) when it is at rest (i.e., when the vesica is not everted).

The aedeagus is encircled by a massive sclerotized ring, the anellus, which is medial to the vinculum and the anterior ends of the valvae. Wide all the way around, the anellus becomes extra wide ventrally (where it incorporates the juxta). Anteroventrally it extends forward beneath the aedeagus, finally forming a pair of short anterior projections (see especially Figs. 2, 3, 5, 7, but also 8–10, 12).

In lateral view *the long, more or less narrow gnathos lies close under the uncus* (Figs. 2, 5, 8–11, 14–16). In dorsal view the uncus suggests a caudally-tapering triangle, but the immediately anterior tegumen fails to prolong the triangular effect (Figs. 1, 4). Distally the uncus splits into paired prongs (interspecifically variable in length) which are in contact or close (Figs. 1, 4).

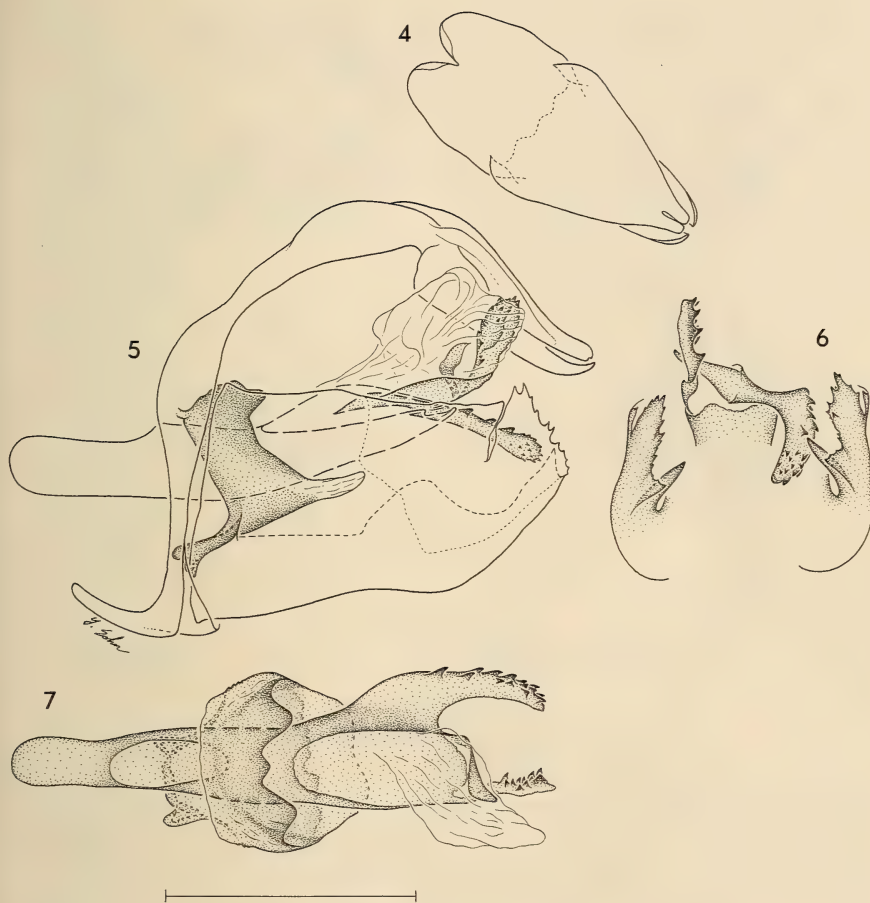
The saccus is short (Figs. 2, 5, 8–16).



FIGS. 1-3. Male genitalia of *Poanes macneilli*, holotype, from east above San Pedro de la Sierra, Sierra Nevada de Santa Marta, 2900-3900 m, COLOMBIA, 7 March 1975, M. J. Adams (genitalic dissection no. X-2352) (USNM). Scale = 1.0 mm. 1, Tegumen, uncus, and gnathos in dorsal view; 2, Complete genitalia (minus right valva) in left lateral view, with anellus and all three titillators stippled and cornutus outlined by dashes (anterior to titillators and medial to anellus); 3, Aedeagus and anellus in dorsal view, with central and left titillators in resting position (folded 180°) and the scouring-pad cornutus showing within the aedeagus (under the top of the anellus).

Female Genitalia (Figs. 17, 18)

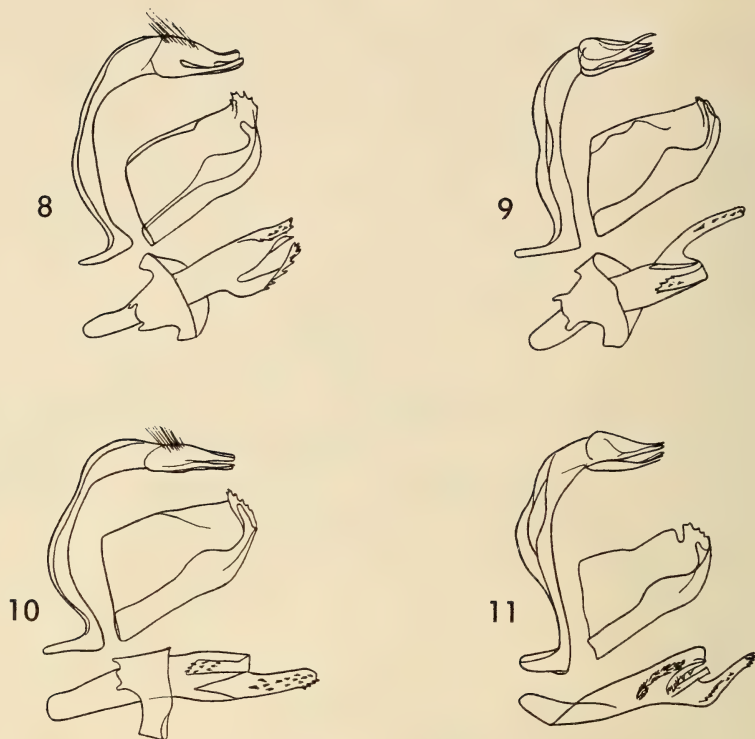
The short, broad ductus bursae initially runs forward but then bends upward (Fig. 18) and to the left (Fig. 17), as well. It is membranous, and usually somewhat longitudinally



FIGS. 4-7. Male genitalia of *Poanes azin* from Bogotá, COLOMBIA, 4 April 1920, F. Clark (X-2965) (USNM). Vesica everted to unfold the flexible central and left titillators, which project from the end of the aedeagus. Scale = 1.0 mm. **4**, Tegumen, uncus, and gnathos in dorsal view; **5**, Complete genitalia (minus right valva) in left lateral view, with anellus and all three titillators stippled; **6**, Distal ends of valvae (showing the outer [dentate], and inner, dorsally-pointing projections on each valva) and aedeagus (showing all three titillators) in posterior view; **7**, Aedeagus and anellus in dorsal view, with central and left titillators unfolded.

wrinkled, both ventrally and dorsally; but it is sclerotized, and transversely wrinkled-and-grooved, laterally. The heavy, conspicuous wrinkles-and-grooves are extremely intricate and not altogether transverse. The ductus bursae does show some ventral sclerotization where it bends upward and some dorsal sclerotization at its origin. There, just above and behind the ostium bursae, a caudally convex shelf—variably sclerotized, and often at least centrally membranous—curves across the midline.

Large, paired, rounded, variably sclerotized and internally spinulose pouches lie just above, behind, and to the sides of the ostium bursae and this arched shelf. After giving



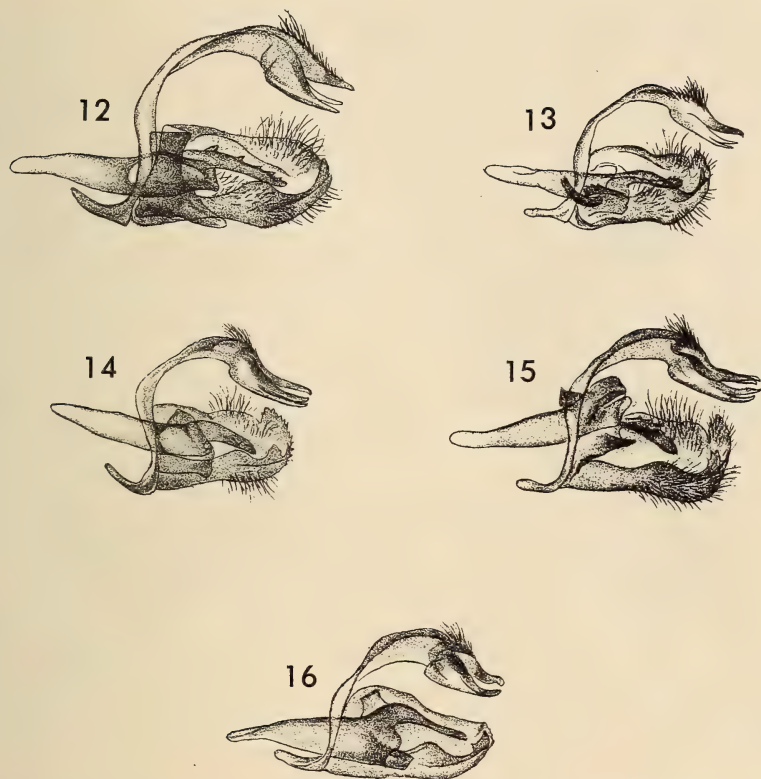
FIGS. 8-11. Male genitalia of four species of *Poanes* ex Skinner and Williams (1924a). All $\times 15$. Drawn from slide mounts in which parts are not perfectly oriented, these exploded figures show (top to bottom) tegumen, uncus, gnathos, vinculum, and saccus in left lateral view; the right valva in medial view (good for seeing the inner, and dentate outer, dorsally-pointing projections); and the aedeagus and anellus in variable views (the anellus, in more or less ventral view when shown, has sometimes rotated relative to the aedeagus; the large, rigid titillator extending backward is always the right one, no matter where it appears). **8**, *Poanes hobomok* from Avon, Connecticut, U.S.A.; **9**, *Poanes zabulon* from Havre de Grace, Maryland, U.S.A.; **10**, *Poanes taxiles* from Chimney Gulch, Colorado, U.S.A.; **11**, *Poanes melane* from southern California, U.S.A. (this figure omits the anellus but shows all three titillators, as well as *melane*'s scouring-pad cornutus which most *Poanes* lack).

rise to the apophyses anteriores, the eighth tergite continues downward to fuse broadly with the dorsal side of each pouch.

From the innermost ends of these pouches, finely spinulose bands extend backward (Fig. 17), diverging through a membranous to very lightly spinulose area, to reach the outer edges of a thick, well-sclerotized, spinulose to centrally bristled transverse element (just in front of the ovipositor lobes), which is variously shaped, particularly along its posterior margin. It usually projects ventrad.

PARATRYTONE GODMAN

Paratrytone is a highly distinct genus that is related to the terrestrial species of *Poanes*. (However, those species of *Poanes* are much closer



FIGS. 12–16. Male genitalia of five species of *Poanes* ex Godman (1900: plate 94), who treated them all as *Atrytone*. Drawn from slide mounts in which parts are not perfectly oriented, these figures show complete genitalia (minus left valva) in left lateral view. Like the Skinner and Williams figures, they present the inner surface of the right valva, whereas mine present the outer surface of the left valva. 12, *Poanes zabulon* (the gnathos has artificially sagged too far below the uncus); 13, *Poanes melane* (again, the gnathos has sagged a bit, but *melane*'s scouring-pad cornutus, which most *Poanes* lack, appears as a dark arc behind the bottom of the vinculum); 14, *Poanes monticola*; 15, *Poanes niveolimbus*; 16, *Poanes inimica*.

to *Ochlodes* than they are to *Paratrytone*—so much so, in fact, that at least terrestrial *Poanes* and *Ochlodes* may ultimately merge.) Males of *Paratrytone* (but also of *Ochlodes*!) have a large stigma on the dorsal surface of the forewing, whereas males of the terrestrial species of *Poanes* do not.

Though I am concerned with all of *Paratrytone*, instead of a subgroup of it, I am drastically changing its composition: six of the nine species included by Evans (1955) must go—four of them to *Poanes*, along with yet another species more recently described and likewise misplaced in *Paratrytone* (see Notes on the Terrestrial Species of *Poanes* below).



FIGS. 17, 18. Female genitalia of *Poanes macneilli* from north of San Sebastian, Sierra Nevada de Santa Marta, 2800–3400 m, COLOMBIA, 15 February 1975, M. J. Adams (X-2365) (collection of C. D. MacNeill). Scale = 1.0 mm. **17**, Ovipositor lobes, eighth tergite with apophyses anteriores, sterigma, and bursa copulatrix in ventral view; **18**, The same, plus the right apophysis posterioris and part of the ductus seminalis, in right lateral view.

The other two species that Evans wrongly stuck in *Paratrytone*—*argentea* (Weeks) from Bolivia and *barroni* Evans from Ecuador—are temporarily without a proper home. (I am setting them in *incertae sedis*, like *simius* Edwards, formerly of *Amblyscirtes* [Burns 1990].) Early in this study I concluded, from Weeks's (1905: plate 15, fig. 2) color paintings of *argentea*, its Bolivian provenance, and its unavailability to Evans (1955:350), that *argentea* did not fit in *Paratrytone*; and eventual dissection of its male genitalia bore me out totally. Evans (1955:351) described *barroni* (in the company of other species that do not really belong in *Paratrytone*) in great superficial detail from a single female from 915–1220 m in Ecuador. I have not gone after this type because neither her looks nor her low latitude and low altitude relate to true *Paratrytone*. Correctly defined and flushed of misfits, *Paratrytone* displays a tidy, restricted geographic distribution that makes biologic sense (see below).

I am also removing the montane Hispaniolan species *batesi* (Bell) which went from *Poanes*, where it was originally described (Bell 1935), to *Choranthus* (Evans 1955), where it had absolutely no business, to *Paratrytone* (Miller 1966), where it has remained (Riley 1975, Schwartz 1989). Even though Miller (1966) examined and compared male and female genitalia of representative species of *Poanes* and *Paratrytone* together with those of all of Evans's species of *Choranthus*, he erred in his placement of *batesi*. Bell (1935) came close to the mark in putting *batesi* in *Poanes*—but not in specifically relating it to *yehl*, *rhaxenor* Godman, *polyclea* Godman, and *aphractoia* Dyar. These last three species, all Mexican, are the only ones of the nine that Evans (1955) had in *Paratrytone* that really belong there. (It is worth noting that *Paratrytone* Godman 1900, with *rhaxenor* as type, should not be confused with its homonym *Paratrytone* Dyar 1905, which, with *howardi* Skinner [=the marsh dweller *aaroni*] as type, is a synonym of *Poanes*.) Having compared KOH-treated genitalic dissections of two pairs of *batesi* with those of *Paratrytone*, *Poanes*, and a dozen species of *Ochloides* (both sexes, 33 dissections), I propose the **new combination** *Ochloides batesi*. As stated above, *Ochloides* and *Poanes* may prove too close for bigeneric comfort. For now it is obvious that the genitalia of *O. batesi*, while different from those of the terrestrial species of *Poanes*, are ever so much nearer to them and especially to those of some species of *Ochloides* than they are to those of *Paratrytone*.

As if in compensation for the near-total purge, *Paratrytone* gets *snowi* (Edwards) (**new combination**) from *Ochloides* plus some undescribed, high-altitude Mexican species (Burns & MacNeill unpubl.). It also keeps *decepta*, one of two species described in *Paratrytone* by Miller and Miller (1972)—but it loses the other one, which belongs with the ter-

restrial species of *Poanes* (see below): figures of the male genitalia (Miller & Miller 1972:figs. 17, 18), despite poor representation of the diagnostic aedeagi, unmistakably show one species in each genus.

To summarize, *Paratrytone* recast contains *rhexenor*, *snowi*, *decepta*, *polyclea*, *aphractoia*, and some undescribed species (one of which, however, is probably *pilza* Evans [1955:343] described as a subspecies of *snowi* from southern Mexico ["Pinal, Puebla, 8000 feet"]).

In *Paratrytone*, as in the terrestrial species of *Poanes*, the genitalia in each sex are clearly variations on a single singular theme. The most salient traits are, in males, two symmetric pairs of aedeagal titillators (one dorsal, one ventral) along with a basally massive gnathos and, in females, a ventrally projecting structure at the back of the lamella postvaginalis (hence distally located, just in front of the ovipositor lobes) that suggests human lips.

In characterizing *Paratrytone* I have studied and compared a total of 86 KOH-treated genitalic dissections (47 males, 39 females). Again, I have honed my working description of each sex while hearing it read aloud as I slowly reexamined each dissection.

Far more limited in geographic and altitudinal distribution than the terrestrial species of *Poanes*, *Paratrytone* is high montane (ca. 2000–3100 m), mostly in Mexico but also in much of the central and southern Rocky Mountains of the United States (extreme southeastern Wyoming, Colorado, New Mexico, and Arizona).

Male Genitalia (Figs. 19–23)

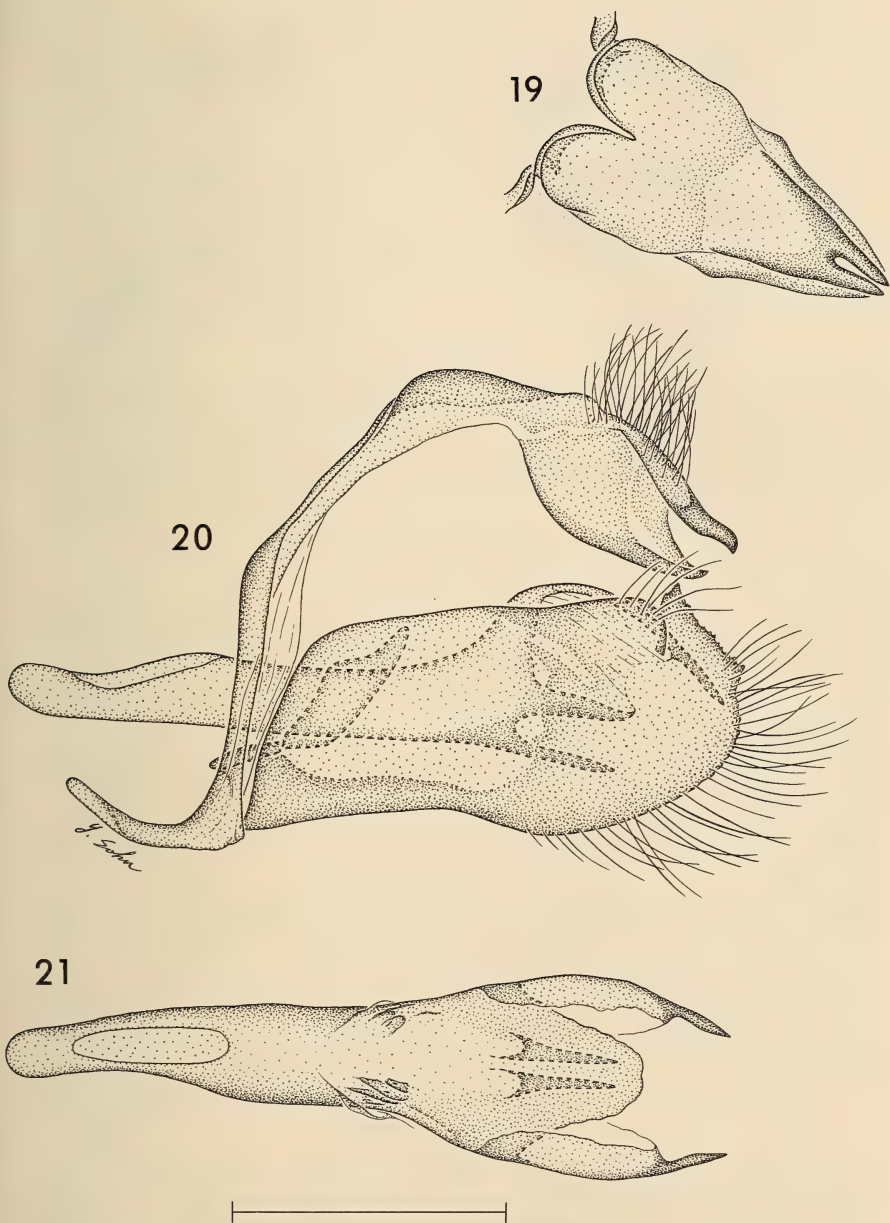
Much as in *Poanes*, the valva in lateral view is roughly rectangular, but its posterior end is sometimes more angled (Fig. 23) than rounded. Again as in *Poanes*, the distal end is set off dorsally from the body of the valva by a vertical slit or notch; but *this end is made up of only one dorsally-pointing projection (which may or may not be dentate)* (Figs. 20, 22, 23). Because *there is no second dorsally-pointing projection arising from its inner surface*, the distal end of the valva is much simpler than it is in *Poanes*.

Two pairs of symmetric titillators spring from the distal end of the aedeagus—one dorsally, one ventrally. All four titillators extend backward (they may also go upward or downward) and all lack teeth, but each ends in a single delicate point (Figs. 20–23). (The titillators vary greatly in length, the ventral pair vanishing in at least one species [*Paratrytone aphractoia*].)

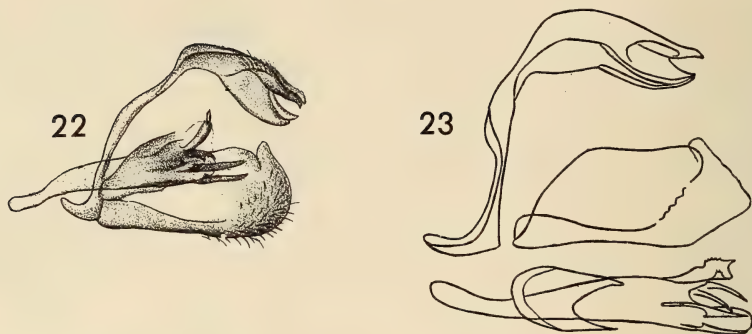
A simple juxta lies ventral and lateral to the aedeagus (Figs. 20, 23), medial to the vinculum and the anterior ends of the valvae. *It is basically U-shaped* (in dorsal or ventral view) with its central, transverse, more or less straight-edged base midventral and its two arms extending backward. Each arm has a single twist, and the arms usually bend dorsally (Fig. 20) but sometimes run straight back.

In lateral view *the gnathos looks massive, especially as it is exceedingly wide proximally* (Figs. 20, 22, 23). Distally it usually departs from the overlying uncus, leaving a wider gap than in *Poanes* (Figs. 20, 22, 23). In dorsal view tegumen plus uncus together suggest an elongate, caudally-tapering triangle. Distally the uncus splits into paired prongs which are medium long and close together (Fig. 19). (It is not "undivided" as claimed by Miller [1966:260].)

The saccus is short, as in *Poanes* (Figs. 20, 22, 23).



FIGS. 19–21. Male genitalia of *Paratrytone* sp. from Cuazimalpa [=Cuajimalpa, ca. 3000 m, 19°21'N, 99°18'W, Distrito Federal], MEXICO, July 1918, R. Mu[e]ller (X-2311) (USNM). Scale = 1.0 mm. **19**, Tegumen, uncus, gnathos, and top of vinculum in dorsal view; **20**, Complete genitalia (minus right valva) in left lateral view; **21**, Aedeagus in dorsal view. Note the two pairs of symmetric titillators, one dorsal and one ventral.



FIGS. 22, 23. Male genitalia of two species of *Paratrytone* ex Godman (1900: plate 93) and Skinner and Williams (1924b). The main problem with these figures, drawn from slide mounts in which parts are not perfectly oriented, involves the aedeagus whose two pairs of symmetric titillators do not adequately show. 22, *Paratrytone rhexenor* from MEXICO; 23, *Paratrytone snowi* from Morrison, Colorado, U.S.A.

Female Genitalia (Figs. 24, 25)

The ductus bursae is short and broad (broader than in *Poanes*)—about the diameter of the corpus bursae where the two join. It runs forward (but not also upward and to the left as in *Poanes*). Lacking the intricate, sclerotized, lateral wrinkles-and-grooves of *Poanes*, it begins at the ostium bursae as a ring of sclerotization, broken dorsally into a pair of sclerotized bands.

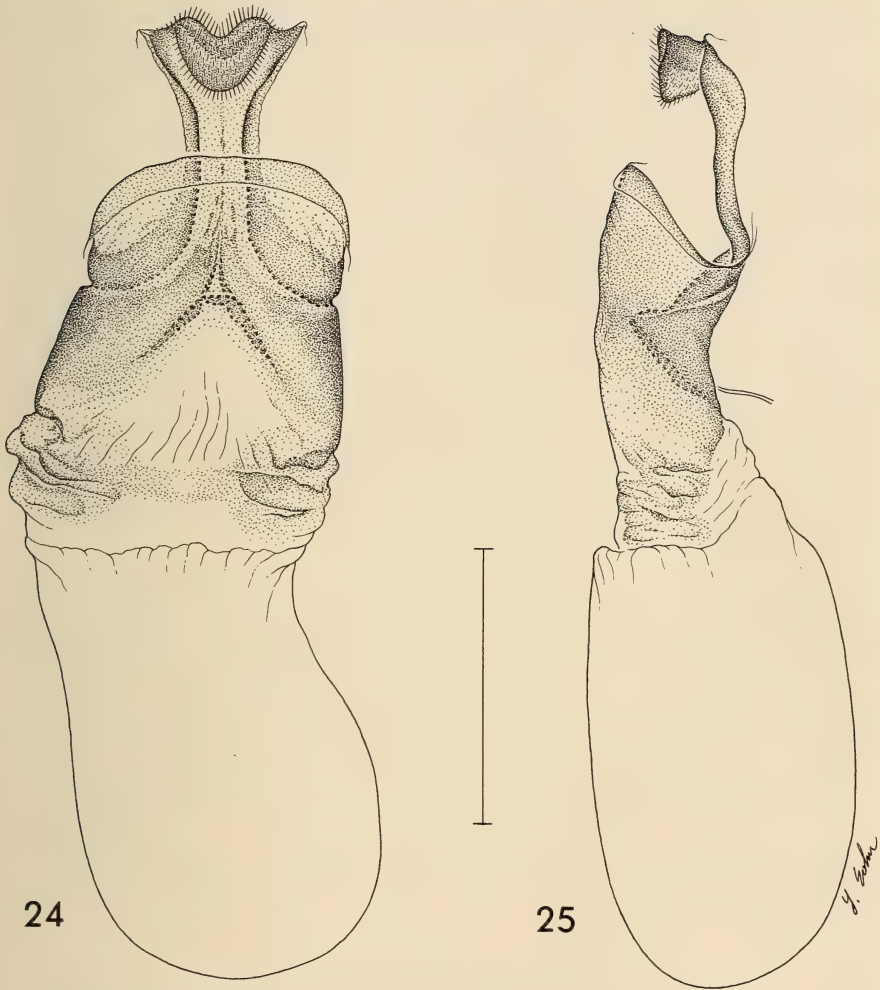
From the ostium bursae, these sclerotized bands initially converge and then diverge—like a pair of parentheses “)” (“ in reverse—as they extend backward the length of the laterally membranous lamella postvaginalis to attach to the upper, outer corners of a thick, heavily sclerotized, spinulose, transverse structure which (just in front of the ovipositor lobes) projects downward, and usually also forward, resembling, in ventral view, human lips.

Anterior to the dorsally broken sclerotized ring around the ostium bursae, the ductus bursae is always well sclerotized dorsally and sometimes variably sclerotized ventrally before becoming membranous. The dorsal sclerotized plate is invaginated middorsally in several species (including the one illustrated [*Paratrytone aphractioia*]). Ventrally, adjacent to the corpus bursae, is a more or less distinctive zone that varies from fully membranous to fully sclerotized. Viewed ventrally, this zone in several species suggests human female breasts or the brassiere that covers them (so that one is tempted to write *Paratytone*).

NOTES ON THE TERRESTRIAL SPECIES OF *POANES*

Poanes melane

I am returning *melane* (Edwards) to *Poanes*. Long ago when Dyar (1905) put only *melane*, *hobomok*, *zabulon*, and *taxiles* in *Atrytone*, the grouping was right but the genus, wrong, because none of those species is its type. Barnes and McDunnough's (1916:132) corrective step—“The species at present placed by Dyar in the genus *Atrytone* we would place, rather than create a new genus, in *Poanes* Scud. along with *massasoit*, with which they seem to possess considerable affinity”—



FIGS. 24, 25. Female genitalia of *Paratrytone aphractioia* from Mexico City, MEXICO, August 1920, R. Mu[e]ller (X-2307) (USNM). Scale = 1.0 mm. **24**, Sterigma and bursa copulatrix in ventral view; **25**, The same, plus part of the ductus seminalis, in right lateral view.

suited subsequent workers such as Lindsey (1921), Skinner and Williams (1924a), Comstock (1927), Lindsey et al. (1931), Bell (1938), and Hoffmann (1941). Skinner and Williams (1924a) went so far as to show the male genitalia of our four terrestrial species of *Poanes* (*hobomok*, *zabulon*, *taxiles*, and *melane*) in a single plate—reprinted in Lindsey et al. (1931) and now here (Figs. 8–11)—where both their distinctive form

and their close similarity leap out. All the same, when Evans (1955), without explanation, switched *melane* from *Poanes* to *Paratrytone*, everyone blindly followed him.

Putting the Californian *melane* back restores *Poanes* in the United States to transcontinental grandeur.

South of the border, *melane* extends to Panama in two superficially defined subspecies—the Mexican *vitellina* (Herrich-Schaeffer) and the Central American *poa* Evans—whose status vis-à-vis nominotypical *melane* warrants further study. Ten dissections of male genitalia indicate that both the lateral and the medial dorsally-pointing projections at the distal end of the valva are shorter and wider in the Californian *melane melane* (Fig. 11) than they are in the more southerly differentiates (Fig. 13), but also that they are longer and narrower in the geographically intermediate *melane vitellina* (dissections from the Mexican states of Veracruz, Puebla, Michoacán, Oaxaca, and Chiapas) than they are in the southernmost *melane poa* (dissections from Costa Rica and Panama)! The apparent polytypic species may be a super-species.

All populations of *Poanes melane* exhibit a well-sclerotized, long and narrow cornutus comprising closely spaced, more or less longitudinal rows of numerous overlapping fine spines set in membrane whose curved shape suggests a cover for, say, the top and upper sides of a tiny caterpillar. It belongs to a more general class that I have dubbed “scouring-pad cornuti” (Burns unpubl.). Missing from most terrestrial species of *Poanes*, this cornutus is so conspicuous in *melane* that it appeared in the Godman (1900) and Skinner and Williams (1924a) figures of *melane* genitalia (Figs. 11, 13) and elicited a remark from Skinner and Williams (1924a:60): “The aedoeagus of *melane* . . . carries . . . a floating bundle of hair-like spines.”

Poanes hobomok

Ranging from southern eastern and central Canada to the northern fringe of the southern eastern and central United States, *hobomok* is the most northern of the terrestrial species of *Poanes*. It seems to pose no genitalic problems. Apart from the tegumen/uncus looking more concave than usual in lateral view (imperfectly shown in Fig. 8), the male genitalia are fairly typical and without obvious idiosyncrasies.

Poanes hobomok is famous for having dimorphic females and for having catalyzed the symbol T_f for duration of copulation (Burns 1970). (The mean T_f of this skipper is $38\frac{1}{4}$ minutes.)

Poanes zabulon and *taxiles*

Claiming that their “abdominal structures [=genitalia] are the same,” Scott (1986:452) made *taxiles* a subspecies of *zabulon*. For such a gen-

itally conservative group, *zabulon* and *taxiles* express what can only be considered major genitalic differences; and the two skippers are undoubtedly distinct species.

The biggest difference is also the easiest to see because it is at the distal end of the male genitalia on the outside of the valva. In *zabulon* a peculiar flap from the body of the valva extends backward, lateral to the lateral (dentate) dorsally-pointing projection, so as to hide it in lateral view (Fig. 26). This condition is unique among the terrestrial species of *Poanes*. In *taxiles* the body of the valva barely overlaps the dentate, dorsally-pointing projection (Fig. 27). And little (Figs. 2, 8, 16) to no (Figs. 5, 11, 13–15) overlap marks all the other species. The striking total overlap in *zabulon* does not show in previously published figures of its genitalia (Figs. 9, 12) because they give inside rather than outside views of the valva. I have verified this difference in many more males of *zabulon* and *taxiles*, from diverse localities, simply by examining the end of the genitalia *in situ*.

A large genitalic difference visible only in complete, KOH-treated dissections involves the posterior margin of the dorsal part of the anellus. Viewed dorsally, it looks in *zabulon* like a very shallow W (much shallower than the one in Fig. 3) but in *taxiles* like a relatively deep, broad U to incipient W (with the point of the W, if present, but slightly developed—not obvious the way it is in Fig. 7).

The medial dorsally-pointing projection at the distal end of the valva is rounded at its tip in both species but broader in *zabulon* than in *taxiles*. This difference, which is subtle, requires oblique views for proper detection; so it hardly shows in the strictly lateral views of Figs. 26 and 27.

Appropriately enough, Bailowitz and Brock (1991:9, 86) treated *taxiles* as a full species, observing that “Some [taxonomic] changes [of Scott 1986] (such as lumping *Poanes taxiles* as a subspecies of *P. zabulon*) go against our conservative grain and are mentioned but not followed.” Despite my stress here on male genitalia, I will add in passing that these two species also differ from one another in aspects of the female genitalia, superficial appearance (amply illustrated in many sources), and size (*taxiles* is larger).

Poanes zabulon is strongly disjunct, ranging through most of the warmer eastern United States from southern New England, the bottom end of the Great Lakes, and southern Iowa to northern Florida and eastern Texas and, in mountains, from southern Mexico (Veracruz, Puebla, Jalisco, Michoacán, Guerrero, Oaxaca, Chiapas) to western Panama (Chiriquí). *Poanes taxiles* is montane from the central and southern Rocky Mountain region of the United States to northern (Durango, Sinaloa) and southern (Jalisco, Veracruz, Puebla) Mexico.

The taxon *psaumis* Godman (1900)—described from two females



FIGS. 26, 27. Left valva of the male genitalia of two species of *Poanes* in left lateral view. Scale = 1.0 mm. **26**, *Poanes zabulon* from Charleson Street, Annandale, Fairfax County, Virginia, U.S.A., 31 August 1979, J. M. Burns (X-3103) (USNM). **27**, *Poanes taxiles* from 0.8 km southeast of Clark Peak, Pinaleno Mountains, 2740 m, Graham County, Arizona, U.S.A., 26 June 1958, J. M. and S. N. Burns (X-3105) (USNM). Note how a caudally-projecting flap from the body of the valva hides the upper part of the dentate dorsally-pointing projection in *P. zabulon* but not in *P. taxiles*. This distal genitalic difference is easily revealed *in situ* by mere brushing of scales or, at most, a bit of dry dissecting.

from Jalisco, Mexico, as a species of *Phycanassa* Scudder (a synonym of *Poanes*) and currently treated as a subspecies of *taxiles*—is the same as *taxiles* (new synonymy).

Poanes azin and *macneilli*

In a two-line footnote to his original description of *psaumis*, Godman (1900:489) unintentionally described *azin*, “an allied form from Colombia . . . but . . . a very much smaller insect.” Half a century later, Bell (1947) described this Colombian skipper again, this time as a subspecies, *richteri*, of *Poanes zabulon*. Ironically, I now find that there really is a second small orange-and-brown species of *Poanes* in Colombia. It and *azin* (= *richteri*) are sisters.

Bell (1947:7) wrote at the end of his description that “The male genitalia are the same as those of typical *zabulon*.” Although wrong, this observation reemphasizes the basic genitalic similarity existing among terrestrial species of *Poanes*.

Poanes macneilli, new species

(Figs. 1–3, 17, 18, 28–31)

Male genitalia. Paired uncus prongs short, in contact only at their tips (Fig. 1). Tegumen/uncus, in lateral view, moderately concave (Fig. 2)—more so than in *azin* (Fig. 5). Overlap between body of valva and lateral (dentate) dorsally-pointing projection small (Fig. 2)—but larger than in *azin*, where it is slight to nonexistent (Fig. 5). Medial dorsally-pointing projection at the distal end of the valva short (Fig. 2). Posterior margin of the dorsal part of the anellus decidedly W-shaped in dorsal view (Fig. 3)—more so than in any other terrestrial species of *Poanes* except *azin*, where the W is much deeper (Fig. 7). Aedeagus with a well-sclerotized, conspicuous scouring-pad cornutus (Fig. 3)—in this respect like *melane* but like no other terrestrial species of *Poanes*. (I have seen a vestigial scouring-pad cornutus in one male of *azin* and one male of *inimica*.)

Female genitalia. Caudally convex shelf that curves across the midline, just above and behind the ostium bursae, narrow, steeply arched, and evenly rounded across the middle (Fig. 17). Large, paired, rounded, internally spinulose pouches above, behind, and to the sides of the ostium bursae mostly membranous, but each with a narrowly triangular stripe of sclerotization tapering (toward the midventral line) across the middle of its dorsal wall (Fig. 17). (This sclerotized stripe continuous dorsally with the eighth tergite—Figs. 17, 18.) Well-sclerotized, spinulose to centrally bristled transverse element, just in front of the ovipositor lobes, wide and shallowly biconcave along its posterior margin in ventral view, with short central bristles (Fig. 17).

Size. Smaller than *azin* and therefore the smallest known species of *Poanes*: forewing length in males 12.6 and 13.2 mm, in female 13.6 mm. Comparative data for *azin*: with 6 males, 1 female at hand, Bell (1947) gave male forewing length as 14–16 mm, female, as 16 mm; with 31 males, 5 females, Evans (1955) reported a male forewing length of 15 mm; both my males measured 14.4 mm.

Facies. Upperside (Figs. 28, 30): A conspicuous vertical dark mark at the distal end of the forewing cell, narrower toward the costal margin and wider toward the inner margin. Large orange areas on both pairs of wings outwardly serrate—not as even as in *azin*. Row of orange subapical spots in spaces 6 to 8 of the forewing more nearly normal to the costal margin than in *azin*; orange spots in spaces 4 and 5 better developed than in *azin*. Orange spot in space 6 of the hindwing smaller than in *azin*.



FIGS. 28–31. *Poanes macneilli* from the Sierra Nevada de Santa Marta of COLOMBIA. (Even numbers, dorsal views; odd numbers, ventral views; all $\times 1$.) **28, 29**, Holotype male; **30, 31**, Paratype female.

Underside (Figs. 29, 31): Much more boldly marked and contrasty than in *azin*, especially on the hindwing, where extremely dark spots (of dark brown overscaled with rust) occur, most notably in the middle of space 1b plus the bases of spaces 2 and 3, toward the base of space 7, and at the base of the wing. A pale median V-shaped band (composed of creamy yellowish spots in males, white spots in the female) runs from space 1c through spaces 2, 3, 4 and 5 (this is the apex of the V, after which is a slight break) to spaces 6 and 7. Pale overscaling (creamy or very light yellowish in males, lilac gray in the female) extends along the upper half of the outer margin of the forewing and along the outer margin of the hindwing as far as the yellow to dull orange abdominal fold.

Holotype. Male. COLOMBIA, Sierra Nev[ada] de S[an]ta Marta, E[ast] above San Pedro de la Sierra, 2900–3900 m, III-7-[19]75; M. J. Adams, Collector; GENITALIA NO. X-2352 J. M. Burns 1987. Deposited in the National Museum of Natural History, Smithsonian Institution (USNM).

Paratypes. Male. Same data as holotype, except genitalic dissection X-2364. Female. COLOMBIA, Sierra Nev[ada] de S[an]ta Marta, N[orth] of San Sebastian, 2800–3400 m, II-15-[19]75; M. J. Adams, Collector; GENITALIA NO. X-2365 J. M. Burns 1987. Both in the collection of C. D. MacNeill.

This new skipper comes from high on a very high (5775 m) and isolated continental “island” (next to the Caribbean Sea in northeastern Colombia), which is famous for its endemism (Adams 1973). True to its name, the Sierra Nevada de Santa Marta is permanently snow-

covered on top and, indeed, still glaciated. Sister species *azin* occurs well to the south, at similar elevations in the Colombian Andes, especially in the region of Tunja and Bogotá.

Poanes niveolimbus, monticola, capta and *ulphila*
(new combinations, all)

This tight complex from montane southern Mexico and Guatemala is a mix of species and synonyms which have long been languishing in *Paratrytone*. The two species *Poanes niveolimbus* (Mabille) and *Poanes monticola* (Godman), although readily separable on the basis of a few stunning superficial features, have practically the same genitalia; I have found almost no consistent differences in a total of 14 male dissections. The modest differences apparent in the dorsally-pointing projections at the distal end of the valva in Godman's (1900) figures of these species (Figs. 14, 15) are individual rather than specific.

In males of this complex, the paired uncus prongs are long and delicate, with fine tips, and are in contact throughout their length (a set of states shared only with *melane*). The tegumen/uncus, in lateral view, is moderately concave (Figs. 14, 15) (about as in *macneilli*). There is little to no overlap between the body of the valva and the lateral (dentate) dorsally-pointing projection (Figs. 14, 15), but much variation in details of expression. The medial dorsally-pointing projection at the distal end of the valva is short (Figs. 14, 15). However, the posterior margin of the dorsal part of the anellus, in dorsal view, looks like an exceedingly flat W in *niveolimbus* but varies from slightly concave (unique among the terrestrial species of *Poanes*) through nearly straight to straight in *monticola*.

Poanes capta (Miller & Miller), described in *Paratrytone* in 1972 from three males and one female from montane Hidalgo, Mexico, is the same as *Poanes monticola* (**new synonymy**). Miller and Miller (1972) admitted that *capta* is very near *monticola* and *niveolimbus* but claimed that it differed from them in minor aspects of distal valval form and dorsal hindwing spotting. Both those characters vary enough that, in a good series of specimens, the supposed interspecific gaps vanish.

Since *capta* is really a *Poanes*, the following behavioral bit from Miller and Miller (1972:5) is of interest: "the few specimens [of *Paratrytone capta*] that were taken . . . did not seem as pugnacious as some *Paratrytone* we have encountered."

Judging from Plötz's four colored figures (copies in USNM), his *ulphila*, described from Mexico in 1883, is also in this complex; but, like specialists before me (Godman 1907, Hoffmann 1941, Evans 1955), I do not know the species. Possibilities run the gamut. At one extreme, with certain allowances for draftsmanship or for biological variation in

the model (neither was likely that wild!), at least two of Plötz's figures could be of *monticola*, in which case the older name *ulphila* would supplant it. At the other extreme, with so much convergence in color pattern among skippers, *ulphila* could be unrelated to the terrestrial species of *Poanes*.

Poanes monticola comes from high elevations in southern Mexico (Veracruz, Hidalgo, México, Distrito Federal, Puebla, Oaxaca); and *niveolimbus*, from high elevations in far southern Mexico (Chiapas) and Guatemala.

Poanes inimica and *lupulina*

On the basis of a very variable color character (the extent of a pale yellow area that begins near the tornus, in space 1b, on the underside of the forewing), Evans (1955) treated *lupulina* (Plötz) as a species distinct from *inimica* (Butler & Druce). I am returning *lupulina* to synonymy. According to geographic data in Evans, *lupulina* lies entirely within the range of *inimica*. Their genitalia strike me as identical.

Though *inimica* (Fig. 16) is plainly one of the boys (Figs. 1–16), its genitalia differ somewhat more (and more obviously) from those of the rest. The paired uncus prongs are long, but stouter than in any other species; and they are in contact only at their tips, which are blunt. The tegumen/uncus, in lateral view, is markedly concave (Fig. 16) (about as in *hobomok*). The medial dorsally-pointing projection at the distal end of the valva is long, but uniquely wide (about as wide as the lateral dorsally-pointing projection) and variously and irregularly truncate (Fig. 16). The posterior margin of the dorsal part of the anellus, in dorsal view, varies from nearly straight to an exceedingly flat W (not unusual). The right titillator is exceptionally long (Fig. 16).

Occurring at moderate elevations from Mexico (Tamaulipas, Veracruz, Hidalgo, Puebla, Morelos, Oaxaca, Chiapas) through Central America (Guatemala, Costa Rica, Panama) to northern South America (Colombia, Venezuela, Ecuador), *inimica* is the most southern of the terrestrial species of *Poanes*.

Fig. 32 conveys at a glance much of what I have done to straighten out the sorry polyphyletic mess in a couple of our heavily used and long stable skipper genera.

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Shifts of species to and from *Poanes* and *Paratrytone*

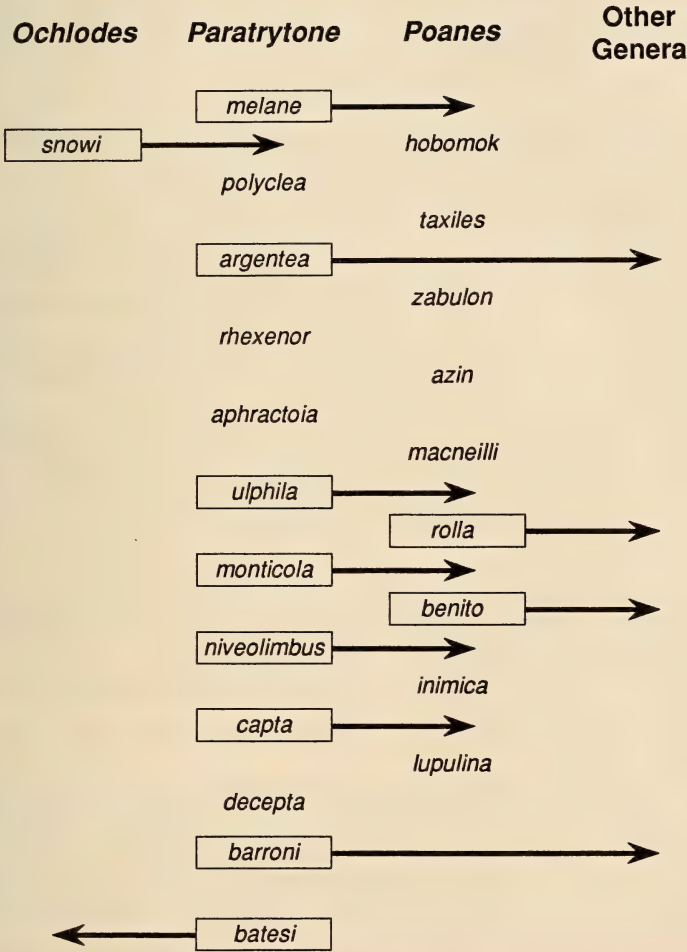


FIG. 32. Summary of species movements made in this paper.

at the American Museum of Natural History unequivocally referred the types of *azin* (Godman) and *zabulon richteri* Bell to the same photos (hence to one and the same species). Richard Robbins, Adrienne Venables, and Elizabeth Klafter dissected genitalia. Daniel Otte, Editor of the *Transactions of the American Entomological Society*, gave permission to reprint genitalic figures from Skinner and Williams (1924a, 1924b). Victor Krantz photographed those figures and others from Godman (1900), as well as the adults of *Poanes macneilli*. George Venable prepared Fig. 32. Young Sohn drew genitalic Figs. 1-7, 17-21, and 24-27 and mounted all figures. Don Harvey brought a couple of papers to my attention. Stan Shetler and the Research Opportunities Fund of the Smithsonian Institution supported relevant fieldwork in Arizona. At home, in the lab, and afield, Sarah Burns helped in ways too numerous or personal to mention.

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MALE MATE-LOCATING BEHAVIOR IN THE COMMON EGGFLY, *HYPOLIMNAS BOLINA* (NYMPHALIDAE)

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ABSTRACT. The mate-locating behavior of males of the common eggfly, *Hypolimnas bolina*, was studied in north Queensland, Australia. Males defended perching sites used in mate location from about 0900 to 1600 h on clear sunny days. Some popular sites contained the larval foodplant, *Sida rhombifolia*, and individual males defended such sites in many cases for several days or more. The form and outcome of interactions between site occupants and intruding males suggested that residents typically win. Observations on site defense by resident males whose color has been altered suggest that color is not important in the maintenance of residence status. These observations and others suggest that male color pattern may be more important in intersexual than intrasexual interactions.

Additional key words: intrasexual competition, coloration, sexual selection, territoriality.

As part of his presentation of sexual selection theory, Darwin (1874) proposed that the brilliant male coloration found in many species of butterflies evolved because of females preferences for brightly colored males. This hypothesis has been discussed frequently in the literature since Darwin (e.g. Turner 1978, Smith 1984). Although empirical evidence for female choice in butterflies is growing (Rutowski 1985, Krebs & West 1988, Wiernasz 1989) and generally supports Darwin's hypothesis, the female-choice hypothesis has had its detractors (e.g. Wallace 1889, Silberglied 1984).

In his review of butterfly reproductive behavior, Silberglied (1984) reiterated and promoted an alternative hypothesis, namely, that brilliant male coloration evolved in another context of sexual selection, male-male competition. Although he did not specify how coloration would act in this context, he clearly thought that male coloration would mediate male-male interactions. If true, this hypothesis should be especially applicable to those butterfly species in which males defend prime positions at encounter sites, and it makes the prediction that alteration of male color will affect the outcome of their interactions with other males.

The common eggfly, *Hypolimnas bolina* Fabricius (Nymphalidae), is a nymphalid butterfly that is widespread in the Indo-Australian region and sexually dimorphic in color. Males of this species are aggressive and site tenacious (Valentine 1989). Here I describe the reproductive behavior of this species, especially patterns of site occupation and defense in males. This was done to evaluate the function of the males' behavior and in conjunction with experiments and observations that bear on the potential role of male color in interactions with conspecifics.

Males of *H. bolina* have a distinctive dorsal coloration throughout



FIG. 1. Dorsal (left) and ventral (right) views of a typical *H. bolina* male (top) and female (bottom).

their range. There is a large white spot near the center of the black background on each wing and a smaller white spot near the tip of each forewing (Fig. 1 top). Each white spot is ringed with violet and the violet extends part way into the white area. The violet coloration associated with the spots is directional and has an ultraviolet component (pers. obs.), as it does in a similarly-colored congener, *H. mistippus* Linnaeus (Nymphalidae) (Silberglied 1984). Females are similar in a general way to males, but they vary in color geographically and their dorsal markings are much less brilliant and clearly defined than male markings (Fig. 1; Clark & Sheppard 1975). In addition, they may have large orange spots on the dorsal wing surface. The ventral markings of males and females are similar.



FIG. 2. A map of the census route on the eastern campus of James Cook University that shows the locations (A–K) of all perching sites used during this study. A through G are in landscaped parts of the campus; H through K are in relatively natural areas of open eucalypt woodland. Legend: BS, Biological Sciences building; GH, greenhouse.

MATERIALS AND METHODS

Study Site and Dates

Field observations were made from January to June 1989, on or within 10 km of the campus of James Cook University of North Queensland, Townsville, Australia. The habitat was an open eucalypt woodland with an understory of grasses. The vegetation was denser along water courses where the common eggfly was found most often. Observations

also were made on males and females in landscaped and watered areas on campus.

Census Techniques

To document where and when males were most often found, a census route (Fig. 2) was established on campus that was approximately 500 m in length and about evenly divided between landscaped and natural habitats. This route was walked hourly for several days to establish the daily pattern of male activity. Each census took about 20 minutes. The location, identity, and behavior (perched or flying) was recorded for each male seen. However, once the basic patterns were established censuses were taken only at 1000, 1200, and 1400 h.

Two techniques were used to identify individual males. Some were marked with numbers on the hindwings using white correction fluid (Swan brand). This was used infrequently as males subjected to the marking procedure usually abandoned the area and were not seen again. The second technique involved the use of distinctive wing wear patterns. I closely approached and inspected perched males and made detailed notes on tears, beak marks, and imperfections that were distinctive and could be used to recognize individuals.

Observations on Interactions

During the censuses written records were made of any interactions that were observed among males. The form, outcome, and, if measured, the duration of each interaction were recorded. In addition, interactions between conspecific males and heterospecifics were observed and recorded during the experiments described below.

Observations on interactions between males and females were made by releasing hand-reared virgin and mated females near perched males in a large (20 m \times 20 m \times 3 m) flight cage and on a few occasions in the field. Females were reared on cuttings of *Sida rhombifolia* Linnaeus (Malvaceae) from eggs obtained from field-caught females in oviposition cages in the lab.

Male Color Alteration Protocol

Three groups of males were established. Untreated males were those that were observed without any handling. Treated males, experimental and control, were removed from their territory at about 1530 h, marked with a black marking pen (Pentel N50 permanent marker), given a white letter with correction fluid on the ventral left hindwing, and placed in a glassine envelope. The envelope was then placed on ice for 90 to 120 seconds. After chilling, the treated male was released onto a leaf or branch about 2 m off the ground. Observations on treated males

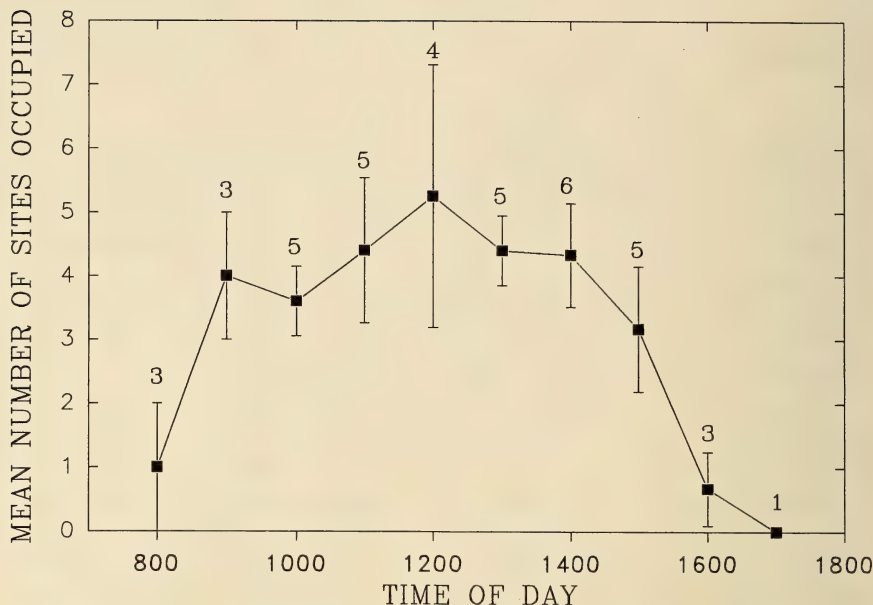


FIG. 3. The relationship between male activity (measured as number of sites occupied) and time of day calculated from data collected 8-10 and 13-15 February 1989. The number over each time period is the number of days of data on which the mean \pm 1 SD are based.

were made the following morning if they appeared at the site of capture. There were two groups of treated males: experimentals which had the black pen applied to the white and violet spots on the dorsal wing surface, and controls which had the black pen applied to black areas on the dorsal wing surfaces.

Observations were made on treated and untreated males by arriving at the site in the morning before the subject male arrived. If another male arrived before the subject male, the intruder was removed. This guaranteed that the subject male could reclaim his site without contest and thereby be the clear resident in all cases. I then remained at the site for several hours observing all interactions that occurred.

RESULTS

Daily Pattern of Activity

The greatest number of males was seen along the census route between 0900 and 1400 h on clear sunny days (Fig. 3). On exceptionally windy or rainy days males were not seen along the census route or elsewhere. Males also disappeared if the weather became poor during the middle of the day.

TABLE 1. Descriptions of perching sites A–K shown in Fig. 3 and their relative frequency of occupation as determined from 52 censuses run between 8 and 20 February 1989. Asterisks indicate sites where *Sida rhombifolia* was found growing.

Site	% Censuses occupied	Description
A*	15.4	Single tree about 3 m high and 10 m from other vegetation
B*	23.1	Two trees about 2–3 m high and 2 m apart
C*	5.8	North side of line of tall (>8 m) trees along carpark; faces out onto lawn
D*	50.0	Same as C
E*	34.6	Same as C
F*	7.7	Same as C
G*	67.3	Tree adjacent to greenhouse
H	1.9	Two small (<3 m) trees at beginning of path
I	5.8	Tree on edge of 2-m-wide path cut through tall grass
J	84.6	Same as I
K	61.5	Tall trees along edge of stream channel

Males were seen more often at some points along the census route than others. The locations of these areas are shown in Fig. 2 and their descriptions and relative frequencies of occupation are given in Table 1. All perching areas included trees with low branches and leaves that were used as perches. There were no other obviously distinctive characteristics of perching sites although some of the most frequently occupied sites included moist, shaded understory areas with dense patches of the larval foodplant (*Sida rhombifolia*), which rarely grew to a height of more than 1 m. Little or no *S. rhombifolia* was found along the path between these sites.

Females were seen on the censuses (Fig. 4) between 0900 and 1500 h in the vicinity of the carpark or the greenhouse. The likelihood of seeing a female on a census did not change with time of day during this period. Most were either resting or ovipositing while perched on the larval foodplant, which was abundant in these areas. Ovipositing females laid a single egg on the underside of a *S. rhombifolia* leaf before flying off.

Male Behavior

Each site was occupied by a single male that when not interacting with a conspecific or other animal perched either on the ground in an open area or, most often, 1 to 2 m or more above the ground on the outer leaves of vegetation adjacent to an open area. From their perches, males flew out and chased flying conspecifics as well as other species of butterflies, including *Cressida cressida* Fabricius (Papilionidae), *Danaus hamatus* Macleay (Nymphalidae), *Euploea core* Macleay (Nymphalidae), *Catopsilia pomona* Fabricius (Pieridae), and *Eurema*

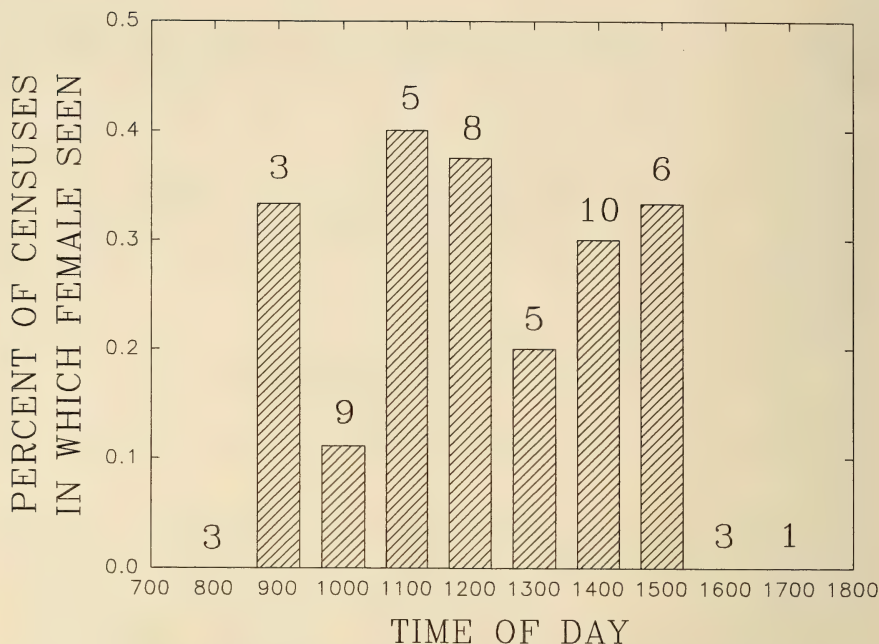


FIG. 4. The likelihood of observing one or more females on a census as a function of the time of day. The number over each bar is the number of days on which censuses were made.

hecabe Butler (Pieridae), other insects (e.g. black dragonflies (Odonata)), and even passing birds. After a chase, a male returned to the original perch or a perch within a few meters of the original.

Interactions between conspecific males in which the resident won varied in duration from 8 to 306 sec (Fig. 5). In interactions of less than 20 to 30 sec, the intruder, chased by the resident, quickly left the area flying with a distinctive flap-glide flight that was not seen at other times. In longer interactions, the intruder turned to face the approaching resident and the two males began flying rapidly around one another. Their wings sometimes clashed audibly during these confrontations. These interactions ended when one male turned and flew off with the flap-glide flight described earlier.

Three lengthy interactions (306, 433, and 675 sec) were observed during the experiments in which the identities and recent histories of the males were known. All three involved treated control males and were between the resident and an intruder that arrived and perched while the resident was on an investigatory sortie or in a fight. For example, a treated control male (T) that was under observation left his perch at site D to chase a crow butterfly (*Euploea core*) for an unusually

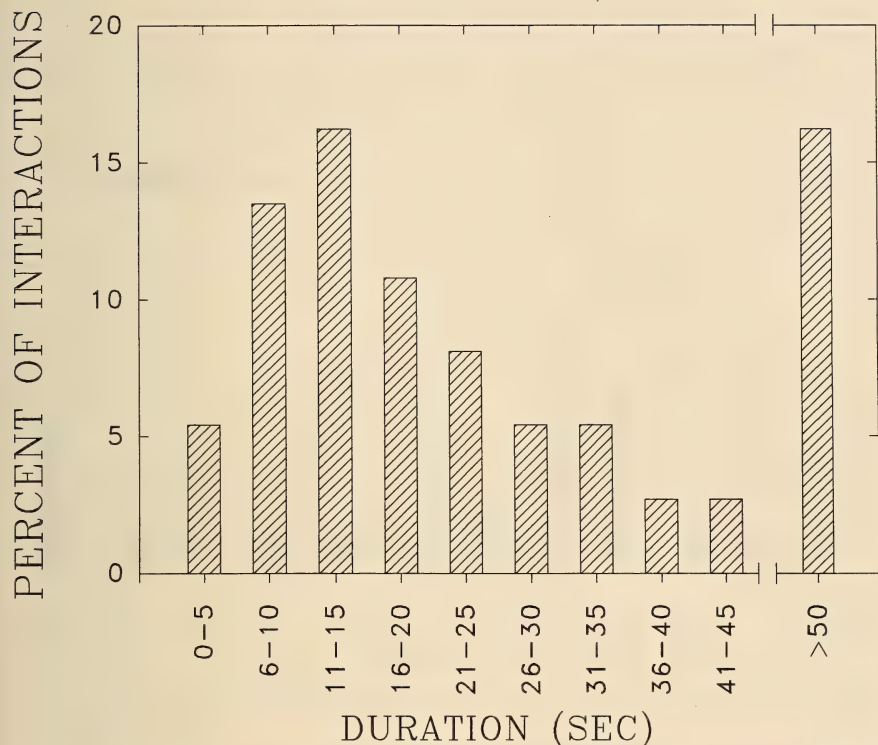


FIG. 5. The relative frequency of interactions of various durations between territorial *H. bolina* males and intruding conspecific males.

long time that exceeded 60 sec. While male T was gone an unmarked male entered and perched in male T's perching area. When male T returned he was approached and chased by the unmarked male. During the next 7 min the males flew rapidly around one another, face to face. After 433 sec, male T flew away using the flap-glide flight.

Interactions with heterospecific butterflies were characteristically brief, lasting only a second or two (Fig. 6). Interestingly, males spent significantly less time chasing butterflies of other species that were white or yellow than they did butterflies that were mostly black (Wilcoxon rank sum test, $P < 0.05$).

Male Site Tenacity

Males typically did not change their defended site within a day's activity period or between days. In 33 cases in which an individual was seen at 1000, 1200, and 1400 h on one day, each was seen at the same perching site at all three times. Males displayed a similar day-to-day

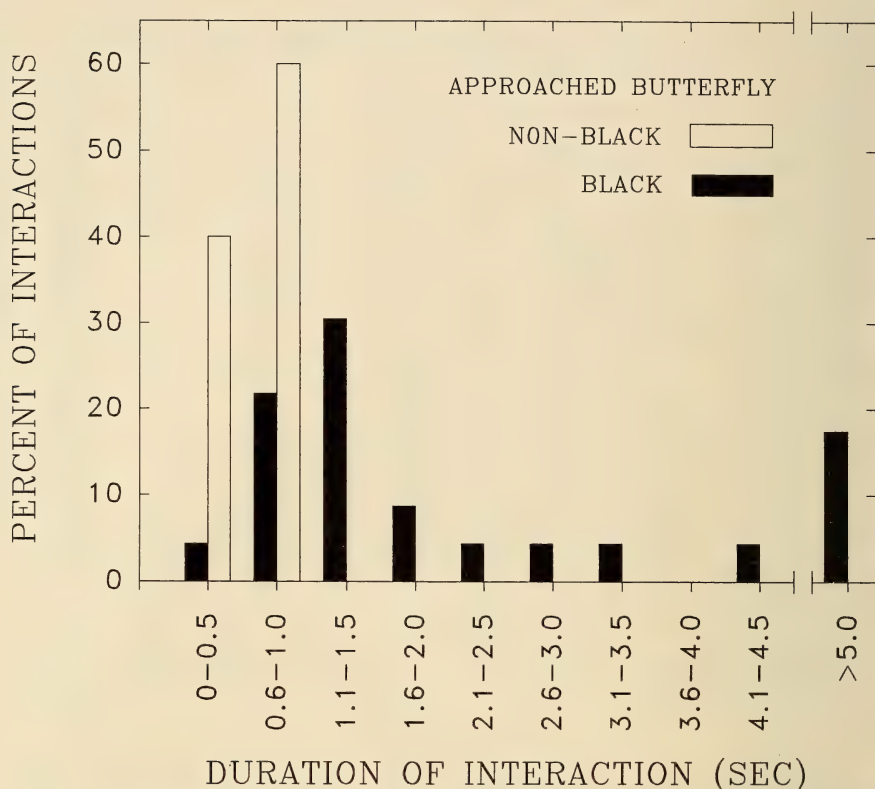


FIG. 6. The relative frequency of various durations of interactions between territorial *H. bolina* males and heterospecific butterflies in two color classes.

site tenacity. In 61 of 67 cases (extracted from records on 17 males) in which an individual was seen on two successive days, he was seen at the same perch site on both days. Five of the six shifts in location between days were made by the male seen over 23 days, but he was always at a site in the same part of the census route (sites D, E, F, and G).

Figure 7 summarizes the observations on all identified males during the 24 days when at least one census was run each day. One male was seen on the census route over a period of 23 days. This graph no doubt underestimates the typical stay of a male in that some data are from males that were treated as part of the experiments and some are from males that were still on the study site when the regular censuses stopped. Also, the natural marks used to identify males may have changed so they were no longer recognizable.

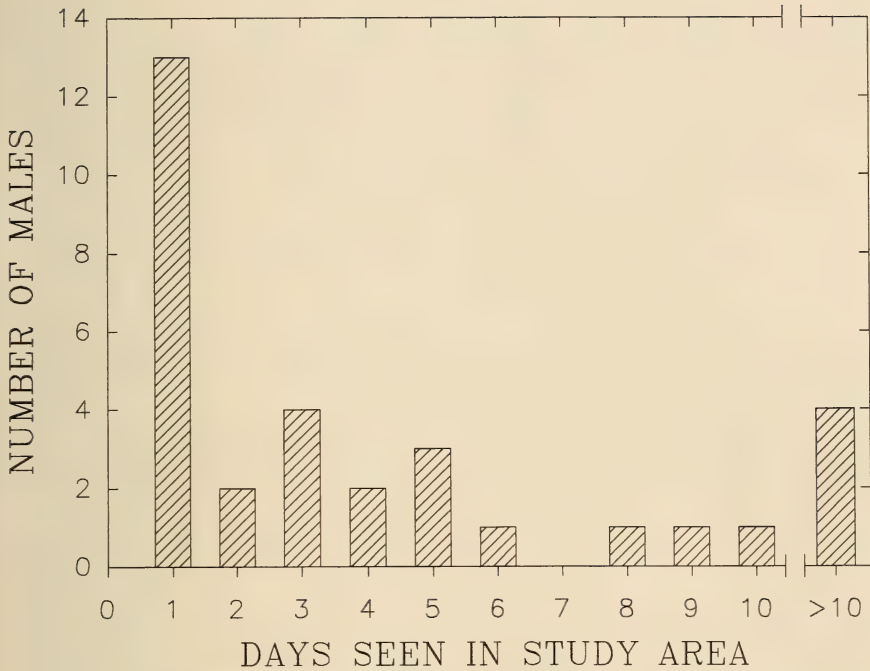


FIG. 7. The tenure of males on the study site for all males during a 24-day period. See text for details.

Observations on Control and Color Altered Males

Although sample sizes are small, the results suggest that resident males are treated as such by intruders regardless of the treatment group to which they belong (Table 2). Even when color-altered, residents readily displaced intruders. Two fights were lost by treated control males but only in circumstances that suggest that they may have lost sole resident advantage by being absent from the site. Male R flew up from his perch to chase a conspecific in an interaction that lasted more than 12 sec and whose conclusion was not seen. While male R was away, two other males were seen fighting near male R's original perch. While these males were fighting, male R returned and perched. The winner of the second fight then flew into male R's perching site and was immediately challenged by male R. The ensuing fight lasted 675 sec and ended with male R leaving the area and the other male returning to male R's original perch. Within a few minutes male R was seen successfully defending another less frequently occupied perching site about 15 m away.

The escalated interaction over site D involving male T was described

TABLE 2. Summary of observations on interactions involving males in various treatment groups that were residents.

Group	Males	No. of fights	Duration of fight		Lost?
			Median	Range	
Control					
Untreated	2	11	18 sec	8-90 sec	0
Treated	3	14	15 sec	3-675 sec	2
Experimental	2	9	10 sec	8-12 sec	0

earlier. Male T lost this fight but returned within 20 min to site D and challenged the unmarked resident. An escalated fight ensued that lasted over 5 min. At the end of this the unmarked male returned to nearby site E and male T flew off but reappeared perched at site D about 12 min later. This interaction was not included in Table 2 because male T's relationship to the site was no longer clear.

Male-Female Interactions: Courtship and Mating

I carefully observed and described, but did not time, fifteen interactions between males and hand-reared females of which four led to copulation. Casual observations were made on several other courtships. Interactions leading to copulation can be summarized as follows. All occurred in cages with hand-reared virgin females and began with the female flying. If the male was perched he flew up from his perch to the female or if flying he approached her from behind. Next, he positioned himself below the female and flew with shallow wingbeats and with the wings spread. The female then alighted and the male, after landing behind but facing the female, moved up alongside her so that his head was about half way along the length of her body. He then curled his abdomen toward the female from between his wings and inserted it between the inner margins of the female's hindwings. In one case, coupling occurred at this time. In the other three, probing by the male caused the female to turn her abdomen away from the male and then fly off. The male pursued and repeated the sequence of events described above. In these cases, coupling occurred only after this sequence was repeated three or more times over what seemed to be a minute or more. Once coupled the male moved to face away from the female.

Unsuccessful courtships ranged from those in which the male flew up and investigated a virgin for only a few seconds before departing to those in which the male followed the pattern for successful courtship described above for up to what seemed to be a minute or more but never succeeded in coupling.

Observations on five mating pairs (courtships not seen for all) produced times from when first seen coupled to when first seen separated of 50, 77, 90, 120, and 129 minutes, which suggests that copulation lasts one to two hours. Three of the females from these pairs were dissected. None contained more than one spermatophore. Using techniques described in Rutowski et al. (1983), I estimated that the males passed no more than 2.6, 3.5, and 3.8 percent, respectively, of their body mass as spermatophore and accessory secretions during copulation.

Three field caught females were dissected, one that was fresh and two that were very worn in appearance. All were mated and none carried more than one spermatophore.

DISCUSSION

Male Mate-Locating Behavior in the Common Eggfly

The behavior of males of the common eggfly is similar in a number of ways to that described for other species in which males have been observed to defend perching sites (Rutowski 1991) including its congener, *Hypolimnas misippus* (Stride 1956). (1) Males select exposed perches on the edge of large open areas. (2) Perched males chase flying males and females. Males are chased for a distance of some meters after which the approaching male returns to his original perch or one nearby. Females are approached and courted. If the female is found to be unreceptive the male returns to his original perch or to one within a few meters. (3) Conspecific males are not tolerated in the vicinity of a perched male. A conspecific male may enter a site and perch undetected, but is chased away as soon as he flies and is detected by the resident. (4) A male typically occupies the same perching site for several days. (5) Perching site preferences are apparently consistent across males; in spite of changes in the identity of the resident the same areas are occupied. (6) Sites contain little or nothing in the way of adult food resources. Males observed during this study were never seen feeding at their perching site. (7) Males pass relatively small spermatophores like those seen in other species that engage in site defense (Rutowski & Gilchrist 1988).

From these observations I conclude that males of *H. bolina* defend perching areas as a mate-locating tactic, that is, to maximize their chances of being the first to detect receptive females. Some features of the sites might make them good places to contact females. First, many sites were along paths or stream beds through the bush. These open paths may be used as flyways by females. Second, many popular perching areas were over shaded areas where the larval foodplant grew and females oviposited. The spermatophore counts from field-caught *H. bolina* females described here and in Ehrlich and Ehrlich (1978; 2

females each with one spermatophore) suggest that females probably do not often mate more than once. Mated females oviposited near male perching sites but during this study no mated female was ever seen to be receptive. Hence, males probably are defending these sites as places where virgin females are likely to be eclosing and taking their first flight, or where virgin females actively go to encounter potential mates.

Defense of encounter sites at or near female emergence areas is known for other butterflies (Rutowski 1991) and does not fall readily into traditional categories such as female defense polygyny or resource defense polygyny (Emlen & Oring 1977). However, because the occupation and defense of sites appears to be important to male reproductive success, males are subject to sexual selection in the context of intrasexual competition. Their coloration may have evolved in this context.

Indications are that in *H. bolina* residents have the advantage in male-male competition as has been observed in other species (Davies 1978, Rutowski 1984, 1991, Thornhill & Alcock 1983). So long as one male is a clear occupant and the other a clear intruder, male-male interactions are brief. Escalated interactions are most likely when both males sense that they are the perching site occupant or resident. This was demonstrated by the several interactions in which one male that had occupied the site for some time returned to the site after an interaction to find another male that had occupied the site in the original male's absence. Escalated interactions have been seen under similar circumstances, sometimes experimentally induced, in a butterfly (Davies 1978, Wickman & Wiklund 1983), a damselfly (Marden & Waage 1990) and a wasp (Alcock & O'Neill 1987).

Male Coloration and the Mating Behavior of *H. bolina*

Data presented here on *H. bolina* and by Stride (1956, 1957, 1958) on *H. misippus* are relevant to the discussion of the role of male coloration in the mating behavior of butterflies. Selection could favor the brilliant coloration of *Hypolimnna* males in intraspecific contexts in three ways. First, intruding males may be more readily stimulated to leave the territory by brilliant coloration in the resident either by making the resident more quickly apparent, making his identity as a conspecific more quickly detectable, or by indicating something about the resident's fighting ability. The results presented here suggest that this is not the case in that intruders left quickly when chased by residents whose color had been altered by obliteration of the most striking pattern components, the white and violet dorsal spots.

Second, intruders may have evolved a coloration that affects the behavior of the residents in some way advantageous to the intruder. Several studies show that intruder color affects resident response. As seen in this study, intruding butterflies that have an overall black ap-

pearance elicit the strongest resident responses. Stride (1956) working with *H. misippus* made the observation that "large pale butterflies . . . appeared to be of little interest to the *Hypolimnias* males" and, using models of various colors, he showed that white models elicited little more than a brief investigatory approach. Stride (1956, 1957) also showed in *H. misippus* that, after the initial approach, males used visual cues to discriminate females from males, i.e. only female coloration elicited courtship. Edmund (1969) showed that one of the female color morphs was especially attractive to males. These results, if anything suggest, the potential for selection against, rather than for, dark colored intruders. On the other hand, brilliant coloration may clearly announce intruder sexual identity and thereby curtail the sexual advances of residents. In any event, the behavior of intruders in territorial interactions does not suggest that intruders attempt to transmit clearly a visual signal.

Third, brilliant male color may be favored in the context of mate choice by females. Male behavior during the aerial phase of courtship is consistent with the notion that a visual signal is being delivered to the female. The position of the male relative to the female and the male's shallow wingbeats clearly display both the white and the directional violet wing markings to the female. Stride (1958) observed the same behavior in *H. misippus* and called it the "quivering flight." He also made a few observations on the response of females to males whose coloration had been altered and to control males. Males rendered colorless by the removal of wings scales were unsuccessful at obtaining matings whereas both control males and males with the white, but not the violet, dorsal wing spots removed were successful in courting females.

Taken together, the various observations on male color and the mating behavior of this genus suggests that female choice may have been important in the evolution of male dorsal coloration. A fruitful line of inquiry would be to design additional experiments to determine if the detection of these markings does affect female receptivity.

ACKNOWLEDGMENTS

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COENOCHROA CHILENSIS, A NEW PHYCITINE MOTH FROM CHILE (PYRALIDAE)

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ABSTRACT. *Coenochroa chilensis* new species is described from Ñuble Province, Chile. Comparisons are made with previously known (three North American and two Brazilian) species. Illustrations include scanning electron micrographs of a denuded head capsule and photographs of the adult moth and male genitalia.

Additional key words: taxonomy, neotropics.

The three male specimens of the new species described below were discovered as a result of recent work sorting and consolidating Neotropical pyralid specimens in the collections of the U.S. National Museum of Natural History [USNM], Smithsonian Institution, Washington, D.C. No female specimens were found, but the males are distinctive in several characteristics and the species is easily differentiated from its congeners.

The genus *Coenochroa* Ragonot 1887 previously was known from three North American (see Shaffer 1968) and two recently described (Shaffer 1989) Brazilian species. In the latter paper I gave a brief review of the genus emphasizing distinguishing features of each species and providing a key. As the new species has the combination of a dentate valva in the male genitalia and no discal spot on the forewing it will not fit the first couplet of that key.

METHODS

Most color designations used below follow the ISCC-NBS Color-Name Charts (Kelly 1965), though for very small structures only general color names could be given. The scanning electron micrographs were taken using a Hitachi S-530 SEM at 15 Kv, the specimens prepared as described earlier (Shaffer 1989).

Coenochroa chilensis Shaffer, new species (Figs. 1-17)

Female. Unknown.

Male. **Head.** Frons light orange-yellow dorsally, dark grayish yellowish brown laterally; protuberance distally cylindrical and relatively narrow (see below), tip about 0.2 times width of frons as measured at midlevel of protuberance. Labial palpus porrect, about 4.3 times as long as eye diameter, basal segment and second segment ventrally yellowish white, second and third segments dark grayish yellowish brown on outer sides. Maxillary palpus (Fig. 8) minute, hidden by labial palpi. Proboscis (Fig. 8) vestigial, hidden by labial palpi. Antenna (Figs. 3-6, 17) filiform, basal two segments of shaft fused, cilia about half as long as segment width. Eye diameter 0.45-0.53 mm (range of the three specimens). Ocellus (Figs. 3, 6, oc) vestigial, minute, conical, lens absent. Vertex light orange-yellow



FIGS. 1-2. *Coenochroa chilensis*. 1, Holotype ♂; 2, Holotype, head, lateral view. Scale bar = 2.0 mm (1), 1.0 mm (2).

between and anterior to antennae, yellowish white posterior to antennae. Occiput dark orange-yellow laterally, pale orange-yellow dorsally. Thorax. Patagium, tegula, and pectus light orange-yellow to dark orange-yellow. Outer sides of prothoracic legs dark brown, on coxa mixed with dark orange-yellow scales. Meso- and metathoracic legs rather uniformly light grayish yellowish brown.

Forewing radius 8.5 mm. R_2 short- to very short-stalked with R_{3+5} , R_5 rather short-stalked with R_{3+4} . M_{2+3} fused, very short-stalked with Cu_1 . Ground light orange-yellow with scattered dark brown scales, these most abundant anterior to cell, astride and posterior to 2nd anal, and along cubitus. Base of cell and base of costa dark brown. Somewhat indistinct white tracing on radius, veins from distal margin of cell, cubitus, and 2nd anal.

Hindwing with two veins reaching outer wing margin from lower outer angle of cell; ground nearly uniformly light grayish yellowish brown.

Abdomen. All sides almost uniformly light grayish yellowish brown.

Male genitalia (Figs. 9-14) with medial process of gnathos (Fig. 12) U-shaped, smooth, lacking serrations. Transtilla a pair of semilunar sclerites at junction of tegumen and gnathos arms (Figs. 13, 14). Juxta nearly square, basal angles rounded. Valva with valvula broadly rounded, distally with small poorly developed blunt tooth on inner margin (Fig. 9, vertical arrow); cucullus with large blunt tooth. Vinculum rounded, lacking developed saccus; sides fused with ventral sclerites of 8th abdominal segment (Fig. 9, horizontal arrow). Aedeagus (Fig. 10) about 7.5 times as long as wide; distal $\frac{1}{6}$ with numerous minute outwardly directed dentations (Fig. 11).

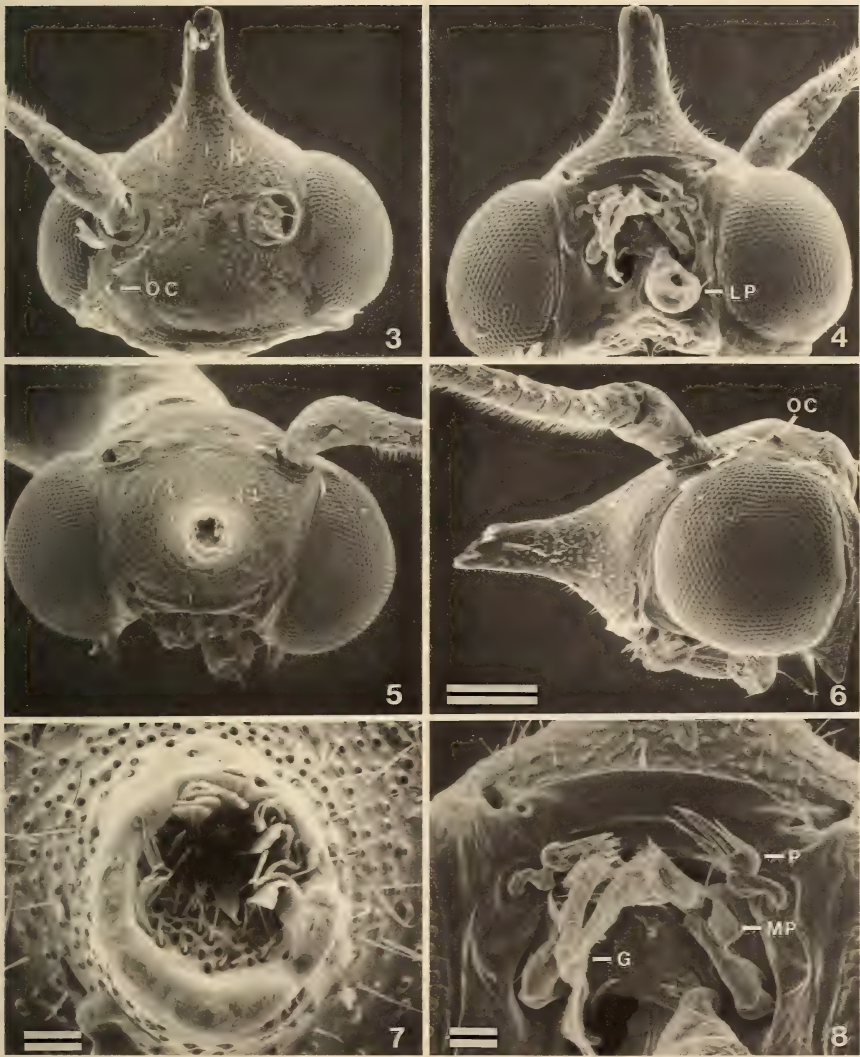
Types. Holotype male (Figs. 1, 2, 9-15), labelled: "CHILE: Ñuble Province near coastal stream 17.5 km. S. Curanipe 25 January 1979, 50 m. D. & M. Davis & B. Akerbergs"; "Genitalia Slide By J. Shaffer USNM 58165"; "Holotype *Coenochroa chilensis* Shaffer, 1992." Two male paratypes with same data as holotype except for slide numbers, first paratype (Figs. 3-8, 16, 17) USNM slide Nos. 58171 (antennae, labial palpus) and 58173 (genitalia of same specimen), second paratype undissected, each labelled: "Paratype *Coenochroa chilensis* Shaffer, 1992" [USNM].

Distribution. Known only from the type locality.

Immature stages and hosts. Unknown.

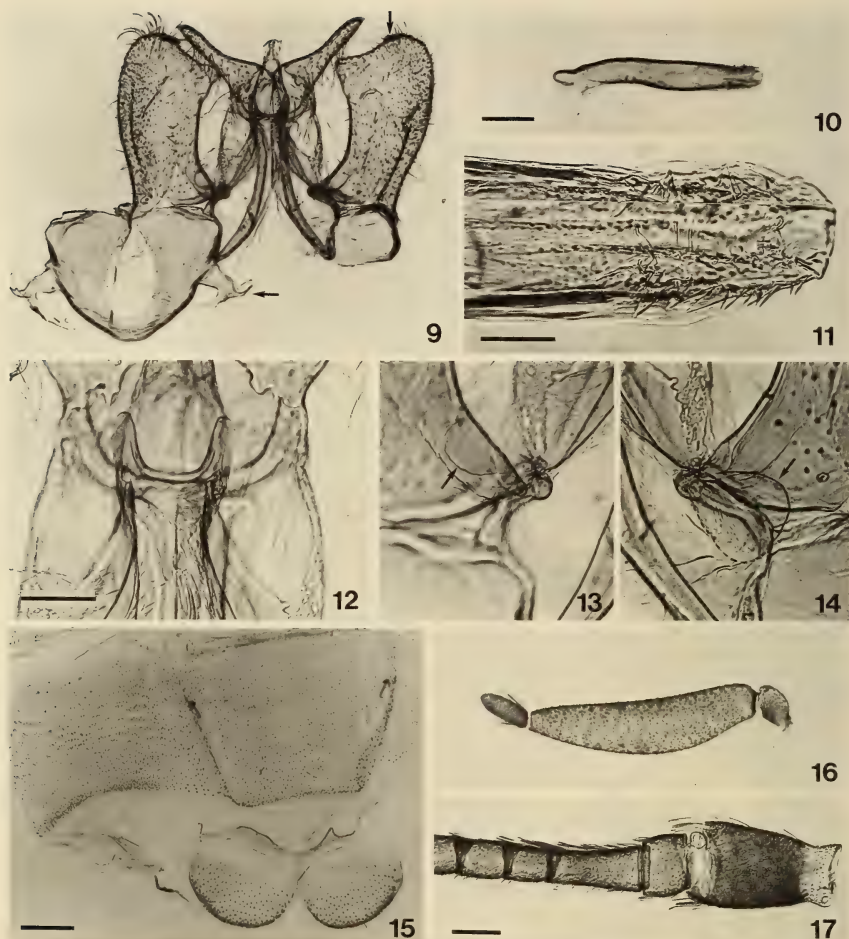
DISCUSSION

Numerous distinctions are apparent when this new species is contrasted with its congeners. The most evident external difference is the



FIGS. 3-8. *Coenochroa chilensis*, paratype ♂, denuded head capsule (G = galea, LP = basal segment of labial palpus, MP = maxillary palpus, OC = ocellus, P = pilifer) in dorsal (3), ventral (4, 8), frontal (5), and lateral (6) aspects. 7, central area of frons protuberance. Scale bar = 250 μ m (3-6), 25 μ m (7), 50 μ m (8).

light orange-yellow forewing ground color, in contrast to the light yellow of other *Coenochroa*. Although this appears to be a clear distinction, it should be noted that wing patterns within the genus, particularly in regard to degree of light vs. dark coloration, exhibit con-



FIGS. 9-17. *Coenochroa chilensis*. 9-15, holotype (USNM slide no. 58165). 9, Male genitalia, aedeagus removed (vertical arrow = cucullus tooth; horizontal arrow = ventral sclerite of 8th abdominal segment); 10, Aedeagus; 11, Aedeagus tip, enlarged; 12, Medial process of gnathos, enlarged; 13-14, Enlargements to show left (up arrow) and right (outlined in ink, down arrow) sclerites of transtilla, 15, Seventh and eighth abdominal segments. 16-17, Paratype (USNM slide 58171) showing labial palpus (16) and basal region of right antenna (17) detached from head shown in Figs. 3-8. Scale bar = 200 μ m (9, 10), 50 μ m (11), 100 μ m (12-14), 250 μ m (15, 16), 50 μ m (17).

siderable intraspecific variation where large series of specimens are available for examination (i.e., the three North American *Coenochroa*). The absence of the forewing discal spot is not a unique character, but is shared only with *C. illibella* (Hulst). Also, the abdomen is grayish in color rather than the yellowish brown of other *Coenochroa*.

In all three (dried and pinned) specimens examined the abdomen was quite flat rather than cylindrical, had a delicate and emaciated aspect, and in fact proved difficult to remove intact. In paratype slide no. 58173 the sclerotized plate bearing the tympanic organs remained attached to the metathorax when the rest of the abdomen was broken away for dissection. It seems likely that this frail condition is characteristic of pinned moths of this species rather than merely an artifact of these three specimens.

The cylindrical tip of the frons is relatively narrow, its width being about 0.20 times the interocular distance as measured at midfrons level. Comparative figures for other *Coenochroa* species range from about 0.35 times in *C. californiella* Ragonot to 0.50 times in *C. illibella*, both North American species, with the Brazilian *C. dentata* Shaffer and *C. prolixa* Shaffer intermediate at about 0.45 times.

The male genitalia exhibit three apomorphies unique to this species of *Coenochroa*: fusion of the two ventral sclerites of the eighth abdominal segment to the sides of the vinculum (Fig. 9, horizontal arrow), a large blunt tooth near the dorso-distal angle of the valva, and minute teeth near the distal end of the aedeagus shaft (Fig. 11).

Don Davis (pers. comm.) reports that the specimens were collected by blacklight about half a mile from the ocean in a relatively undisturbed habitat occupying a ravine. The surrounding countryside upland of the ravine was dry, treeless, and very disturbed, the only trees in the region being confined to ravines. The soil everywhere, both in and above the ravine, was sandy. The last point is of interest as the distribution of *Coenochroa* species suggests an association with sandy soil habitats.

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PARADULCEDO, A NEW GENUS OF SATYRINAE (NYMPHALIDAE) FROM WESTERN COLOMBIA

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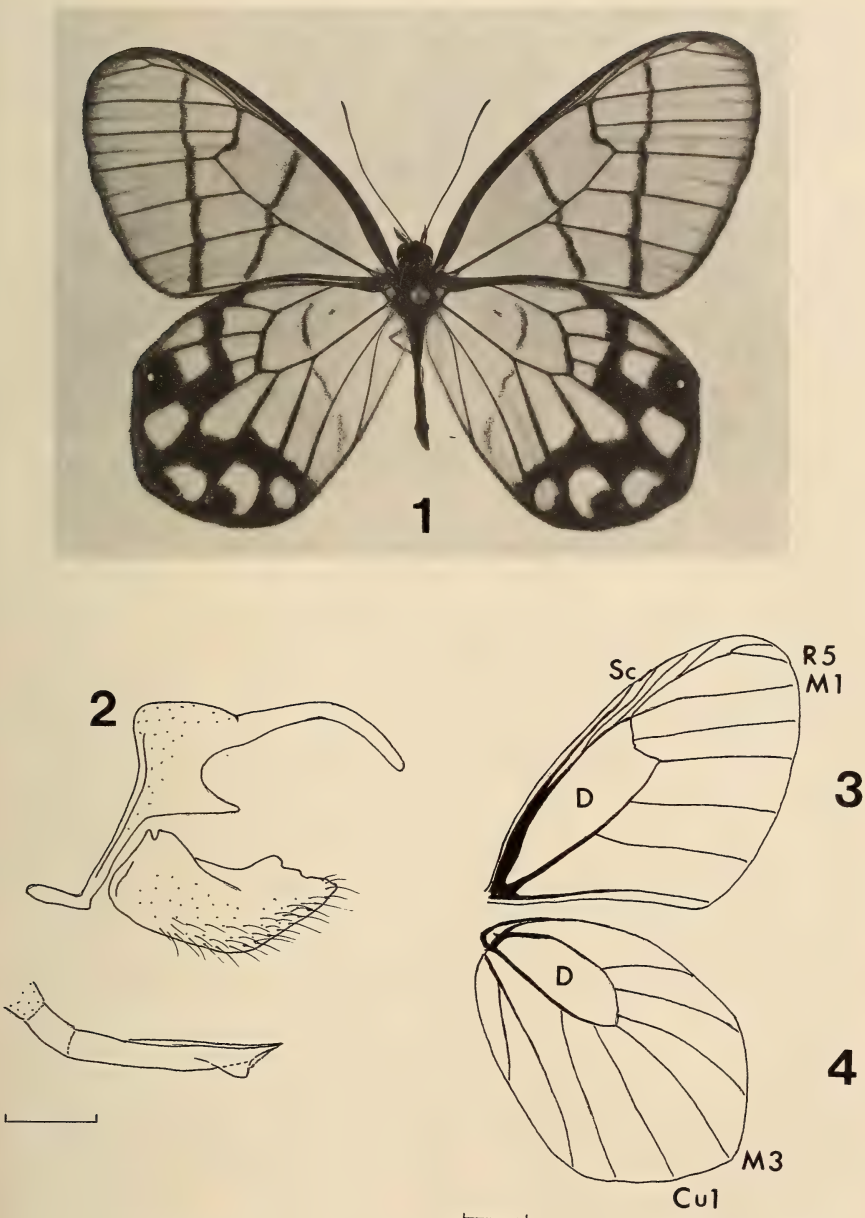
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ABSTRACT. *Paradulcedo*, new genus, is proposed for the satyrid butterfly originally described as *Callitaera mimica* Rosenberg & Talbot. This little known species, endemic to western Colombia, has long been considered a member of the genus *Cithaerias*, from which it is quite distinct. Descriptions of the wing venation and male genitalia are given. *Paradulcedo* is compared to members of the genera *Dulcedo*, *Pseudohaetera*, *Haetera*, *Cithaerias*, and *Pierella*.

Additional key words: *Dulcedo*, *Pseudohaetera*, *Haetera*, *Cithaerias*, *Pierella*.

The tribe Haeterini contains five genera: *Cithaerias* Hübner, *Dulcedo* d'Almeida, *Pseudohaetera* Brown, *Haetera* Fabricius, and *Pierella* Herich-Schaeffer. All five are confined to the Neotropical Region (Miller 1968, Masters 1970, Smart 1976, D'Abrera 1989) and all occur in Colombia. The butterflies of this tribe are, for the most part, readily distinguished from all other groups of the Satyrinae by having largely transparent wings with one or two ocelli and patches of color on the hindwing margin. The only exception to this description is the genus *Pierella* which has brown coloration on the upper wings and brilliant patches of color on the hindwing distal area with a variable number of ocelli. The genus *Dulcedo* is monotypic containing the single species *D. polita* (Hewitson, 1869) (Fig. 11), which ranges from Nicaragua to Western Colombia (DeVries 1987). The genus *Pseudohaetera* also contains a single species, *P. hypaesia* (Hewitson, 1868), distributed from Colombia to Bolivia (Weymer 1924, Brown 1942, Smart 1976) where it is confined to the Andean region between 1200–2500 m. This species is the only known high-altitude haeterine butterfly found commonly in cloud-forest relicts above 2000 m (Fig. 12). In Colombia, *P. hypaesia* occurs on the east slope of the western cordillera and on the central and eastern cordillera (J. A. Salazar pers. comm.).

In the last ten years, butterfly collectors working on the west side (Pacific slope) of the western cordillera have found a species that closely resembles *P. hypaesia* both in the color markings on the hindwing and in flight behavior. Rosenberg and Talbot (1914) described this species as *Callitaera mimica* from specimens collected at La Selva, located at 1400 m on the upper San Juan River, Chocó, Colombia. This rare and poorly known species, endemic to western Colombia, has been retained in the genus *Cithaerias* virtually since its original description, and was listed in *Cithaerias* by D'Abrera (1989). Takahashi (1981), in a list of Haeterinae collected by two Japanese expeditions to Colombia, did not



FIGS. 1-4. *Paradulcedo mimica* (Rosenberg & Talbot). 1, ♂ adult, upper side. 2, ♂ genitalia, lateral view with aedeagus removed (aedeagus, lateral view, beneath). 3, ♂ forewing venation. 4, ♂ hindwing venation. Scale lines = 1 mm for Fig. 2 and 5 mm for Figs. 3-4.

mention this species. In the most recent treatment of Neotropical Satyridae (D'Abrera 1989), the male type of *C. mimica* Rosenberg & Talbot is illustrated. Keith S. Brown Jr. (pers. comm.) suggested that *C. mimica* could belong to the genus *Dulcedo* based on superficial observations.

As members of neither *Cithaerias* nor *Dulcedo* are believed to exist above 1500 m in the Andean mountains and because they have distinctive flight behaviors, I began a detailed study to determine the proper generic affinities of *mimica*. Comparisons of the genitalia, wing venation, and adult behavior of *C. mimica* with those of species representing its close relatives, *Dulcedo*, *Cithaerias*, *Haetera*, *Pseudohaetera*, and *Pierella*, suggests that *C. mimica* does not belong to either *Cithaerias* or *Dulcedo*. The results of these studies led to the conclusion that *C. mimica* should be placed in a new genus closely related to *Dulcedo* and *Pseudohaetera*. I therefore propose the following new genus.

***Paradulcedo* Constantino, new genus**

(Figs. 1–4, 5, 10, 22)

Type species: *Callitaera mimica* Rosenberg & Talbot, 1914:677.

Cithaerias mimica (Rosenberg & Talbot); D'Abrera, 1989:740.

Cithaerias gilmouri Okano; Okano, 1986:1.

Description. Male and female with same wing color pattern; female larger. **Eyes:** Naked, black-copper in life. **Palpi:** Slender, appressed to head, not extending beyond frontal vestiture; third segment small, one-seventh length of second. **Antenna:** Slender, eight-tenths length of forewing discal cell, comprising 47–48 segments, the terminal 7 slightly compressed without forming a club. **Forewing** (Figs. 1, 3): Completely transparent with two strong lines running across; wing shape rounded (elongated in *Cithaerias*); M_1 and R_{3+5} connate at the point of origin from the discal cell (D) (in *Cithaerias* M_1 departs from R_{3+5} and not from D; in *Dulcedo* M_1 and R_{3+5} arise independently from the discal cell). **Hindwing** (Figs. 1, 4): Transparent with black markings (actually a strong, wide submarginal line) similar to *Pseudohaetera*; viewed ventrally, the markings are brown in *Pseudohaetera*, black in *Paradulcedo*; two ocelli on the hindwing margin (*Cithaerias* and *Dulcedo* have one); M_3 curved, originating from discal cell (M_3 straight in *Cithaerias*); Cu_1 and M_3 originating separately from discal cell (arising from same point in *Pseudohaetera* and *Haetera*); discal cell acute distad (rounded in *Dulcedo*). Length of forewing (from base to apex): male, 23.5 to 26.0 mm ($n = 11$); female, 28.0 to 32.0 mm ($n = 6$).

Male genitalia (Fig. 2): Uncus curved and elongate without lateral projections (in *Dulcedo* there are lateral projections or horns); gnathos small (large and prominent in *Cithaerias*); aedeagus pointed apically (rounded in *Dulcedo*, Fig. 5; Table 1).

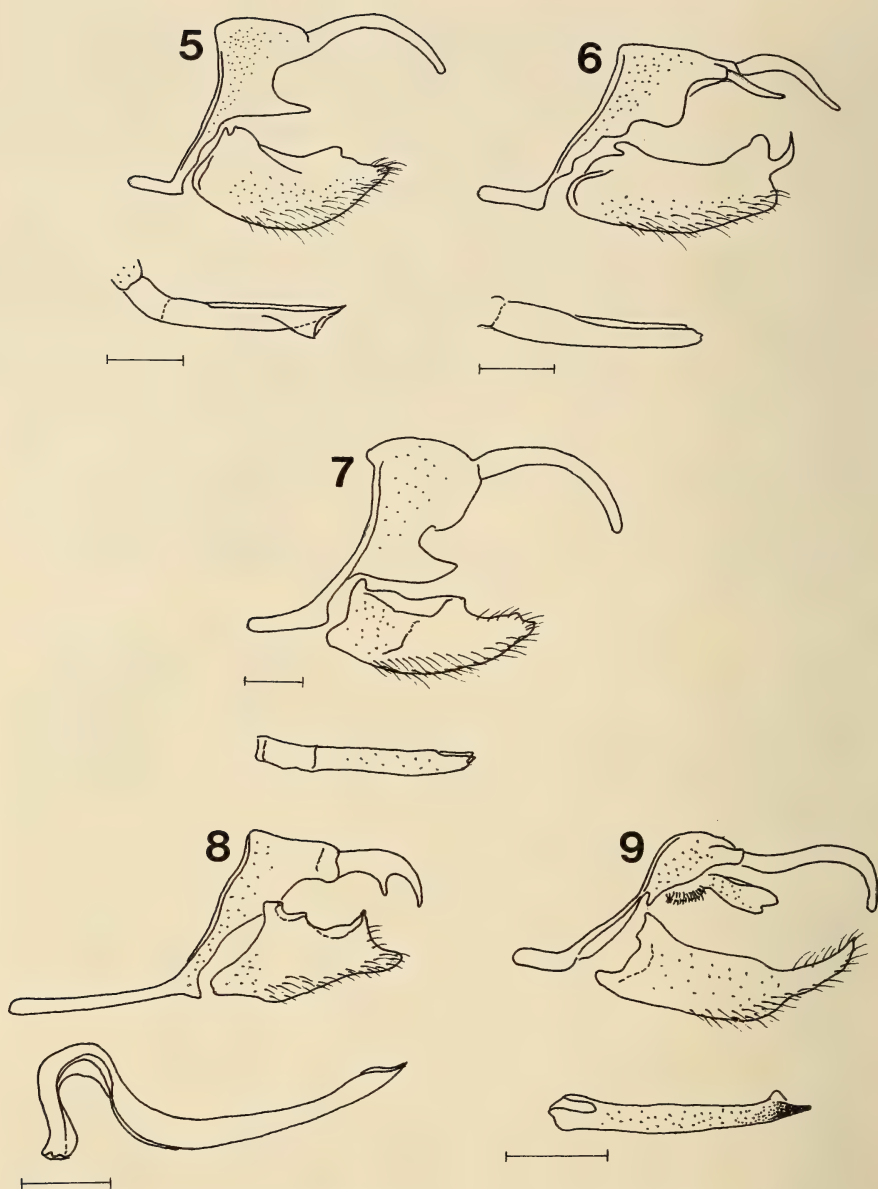
Relationships. Morphologically, *Paradulcedo* can be separated from *Cithaerias* by the characters noted in the description above. Although the wing venation of *Paradulcedo* shows affinities with *Dulcedo*, differences in genitalia indicate that they are not congeneric. On the other hand, the genitalia of *Paradulcedo* reveal affinities with *Pseudohaetera*, but the wing venation is quite different.

Type specimens. Lectotype, ♂ and ♀ COLOMBIA: Chocó Dept., La Selva (Pacific slope), upper San Juan River, 1400 m (BMNH). Paralectotypes: All from Colombia, 1 ♂, 1 ♀, Risaralda Dept., Pueblo Rico, 1580 m (BMNH); 1 ♂, Risaralda Dept., Siato, 1585 m (BMNH). All type material is in the Natural History Museum, London (BMNH).

Additional specimens. COLOMBIA: CHOCÓ: San José del Palmar, 1000 m, 2 ♂ (J. H. Velez) (Museo de Historia Natural, Manizales), 2 ♀ (J. A. Salazar leg.), 1 ♂ (J. F. Lecrom

TABLE 1. Morphological characters to differentiate *Paradulcedo* from *Cithaerias*, *Dulcedo*, *Haetera*, *Pseudohaetera*, and *Pierella*.

Character	Genus				
	<i>Paradulcedo</i>	<i>Cithaerias</i>	<i>Dulcedo</i>	<i>Haetera</i>	<i>Pseudohaetera</i> <i>Pierella</i>
Hind wing venation	M ₃ curved	M ₃ straight	M ₃ as in <i>Paradulcedo</i>	M ₃ with curve very pronounced	M ₃ with curve less pronounced
	Cu ₁ and M ₃ from the discal cell departing separately	Cu ₁ and M ₃ separated at origin	Cu ₁ and M ₃ separated at origin	Cu ₁ and M ₃ con-nate at origin	Cu ₁ and M ₃ con-nate at origin
	Discal cell (D) acute distad	D more elongated than <i>Dulcedo</i> and <i>Paradulcedo</i>	D rounded distad	D wider than <i>Pseudohaetera</i>	The point where M ₃ and Cu ₁ depart is more acute than in <i>Haetera</i>
Number of ocelli	2	1	1	2	2
	Uncus curve and elongate	Uncus long and curve apically	Uncus curve and elongate. There are lateral horns	Uncus short and curve. Has a tooth	Uncus curved and elongate as in <i>Paradulcedo</i>
	Gnathos small, not visible laterally	Gnathos large and prominent	Gnathos small	Gnathos small	Gnathos small
Male genitalia	Aedeagus straight and apically pointed	Aedeagus straight and pointed; tip heavily sclerotized	Aedeagus rounded apically	Aedeagus long and n-shaped basally; pointed apically	Aedeagus straight and rounded apically
	Upper wing with two bands.	Hindwing transparent with patches of color or	Hindwing transparent with narrow submarginal lines	Upper wing with one band. Hindwing transparent with a strong black submarginal line as in <i>Paradulcedo</i>	Upper wings brown with patches of color on hindwing
	Hindwing, transparent with a wide black submarginal line				



FIGS. 5-9. Male genitalia comparisons of five haeterine genera from Colombia. 5, *Paradulcedo mimica* (Rosenberg & Talbot) lateral view of genitalia with aedeagus removed (aedeagus, lateral view, beneath) Alto Calima, Valle. 6, *Dulcedo polita* (Hewitson), Alto Anchicayá, Valle. 7, *Pseudohaetera hypaesia* (Hewitson), Peñas Blancas, Farallones de Cali, 2000 m. 8, *Haetera piera* (Linnaeus), Río Amacayacu, Amazonas. 9, *Cithaerias aurorina* (Weymer), Puerto Nariño, Amazonas. Scale lines = 0.5 mm.

leg.); El Tabor, 1 ♂ (J. F. Lecrom leg.); RISARALDA: Santa Cecilia, 900 m, 1 ♀ (J. H. Velez) (MHNM); San Antonio del Chami, 1600–2000 m, 2 ♀ (J. A. Salazar leg.); VALLE: Rio San Juan, km 56, 1200 m, 2 ♂, 6. viii. 1985 (L. M. Constantino leg.); Calima III, 1400 m, 1 ♂, 16.v.1984 (E. Constantino leg.); Alto Rio Pepitas, 1600 m, 1 ♂, 15.vi.1986 (M. Linares leg.); cerro Los Chancos, 1600 m, 2 ♂, 1 ♀, 10.vii.1983 (J. I. Martinez leg.); Rio Bravo, Calima, 1300 m, 1 ♂, 12.iv.1985 (L. M. Constantino leg.).

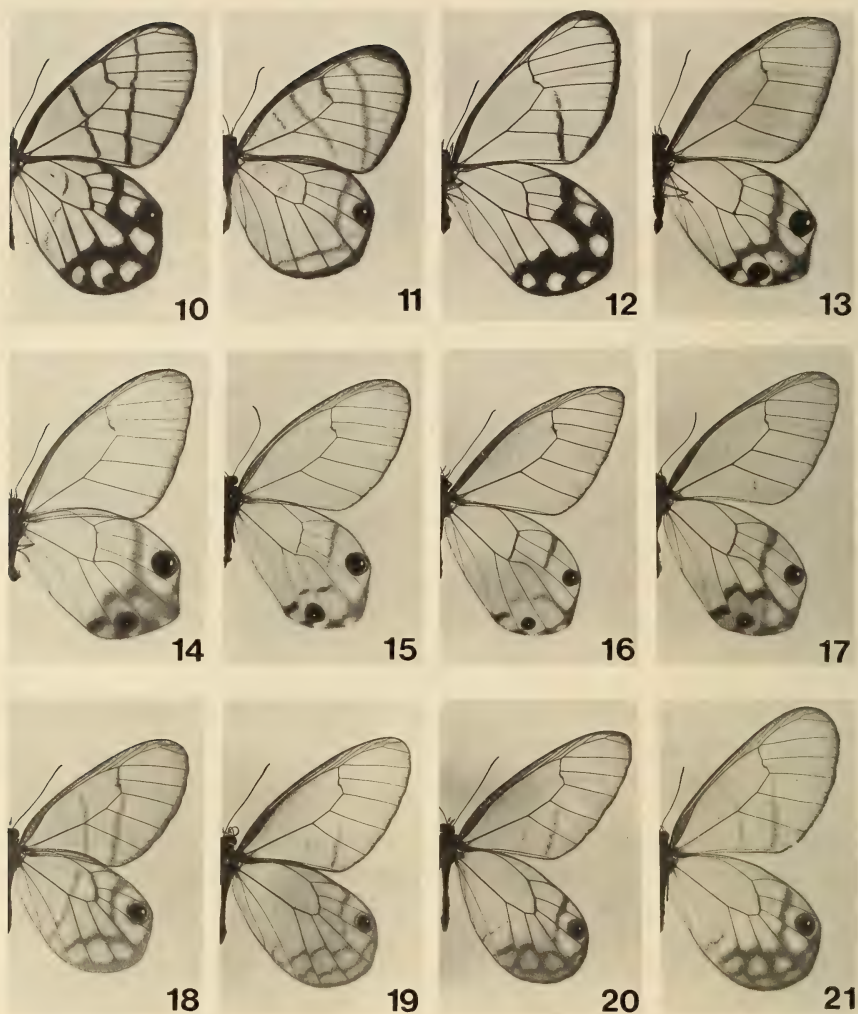
NATURAL HISTORY

Paradulcedo mimica is restricted to undisturbed premontane and montane forest (commonly cloud-forest relicts) on the west side (Pacific slope) of the western cordillera between 900 and 1600 m, with a mean annual precipitation of 5000–6000 mm. Its geographic distribution ranges from Chocó to Cauca (Fig. 22). The range may include Nariño and northwestern Ecuador, but there are no specimens reported from these two regions. The flight behavior is very similar to that of *P. hypaesia*, characterized by being slow and erratic, whereas that of *Dulcedo polita* (which occurs locally on the Pacific Coast in association with pluvial forest from sea level to 1000 m) is very fast and straight. Flight activity of *P. mimica* is during day light hours, from 1000 to 1500 h for males and from 1300 to 1600 h for females. The flight period is restricted mainly to the dry season between June and August, but in some years *P. mimica* can be found during the first rainy season between March and May. Despite many hours of field observation, neither courtship nor oviposition activities were observed, so the larval food plant and immatures remain unknown.

DISCUSSION

My field observations of *P. mimica* over the last five years indicate that it is restricted to a narrow transitional habitat on the Pacific drainage between montane cloud forest and the foothills of the western cordillera. This habitat, which I term the “belt of endemism,” shows a high degree of endemism and biotic peculiarity for butterflies, plants (Gentry 1982), and birds (Haffer 1967), in contrast to other areas of Colombia. This perhaps is an indication that *P. mimica* is an endemic Colombian species. The known distribution of *P. mimica* (Fig. 22) agrees with the “Chocó Quaternary Refugia” proposed for neotropical lepidoptera by Brown (1975). Very likely the Chocó region was a “forest refugium” during pleistocene glaciations (Brown 1982), explaining the occurrence of a high number of endemic butterflies there and in immediately adjacent areas. The Chocó region is located on the Pacific slopes of the western cordillera of Colombia from north of Quibdó to near Lago Calima, across Upper Atrato and San Juan River systems, and its influence is seen as far south as central-western Ecuador (Brown 1975).

Although *P. mimica* was so named because of the black markings of



FIGS. 10-21. Wing venation of some haeterine species from Colombia. Note the shape variation of the hind wing discal cell and the vein M_3 for each genus. **10**, *Paradulcedo mimica* (Rosenberg & Talbot) ♂, Alto Calima, Valle. **11**, *Dulcedo polita* (Hewitson) ♀, Rio Tatabro, Bajo Anchicayá, Valle. **12**, *Pseudohaetera hypaesia* (Hewitson) ♀, Peñas Blancas, Farallones, Valle. **13**, *Haetera macleannania* Bates ♂, Rio Tatabro, Valle. **14**, *Haetera macleannania* Bates ♀, Rio Raposo, Valle. **15**, *Haetera piera piera* (Linnaeus) ♀, Leticia, Amazonas. **16**, *Haetrera piera ecuadora* Brown ♂, Puerto Umbria, Putumayo. **17**, *Haetera piera ecuadora* Brown ♀, Orizá, Putumayo. **18**, *Cithaerias menander* (Drury) ♂, Rio Sabaletas, Valle. **19**, *Cithaerias aurorina* (Weymer), ♂, Puerto Nariño, Amazonas. **20**, *Cithaerias pyritosa* ssp. (Clifton ms.) ♂, Villavicencio, Meta. **21**, *Cithaerias pyritosa* ssp. ♀, same locality.

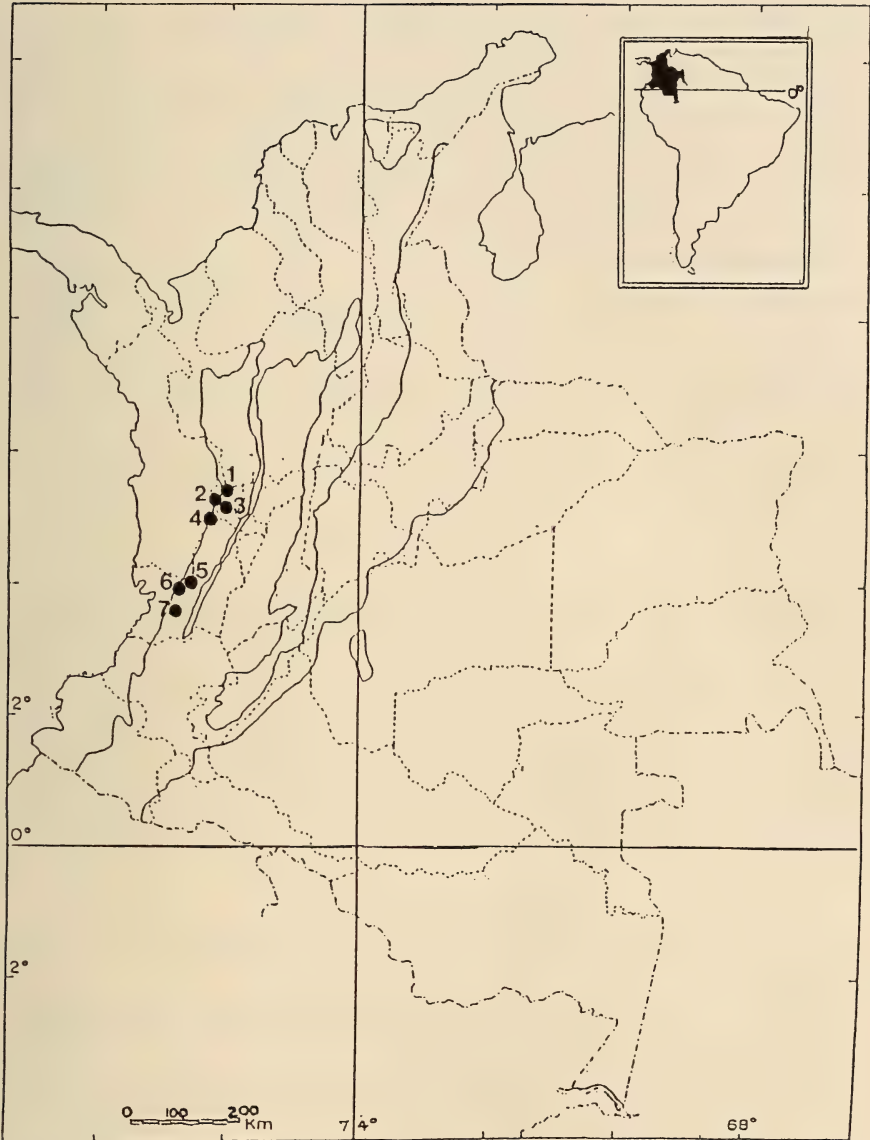


FIG. 22. Known distribution of *Paradulcedo mimica* in Colombia. 1, Risaralda, San Antonio del Chami, 1600–2000 m. This locality is the farthest north known for *P. mimica*. The habitat where the collections were made is on the upper Mistrato River in montane cloud forest. 2, Risaralda, Santa Cecilia. On the west side (Pacific slope) of the western cordillera in premontane cloud forest. 3, Risaralda, Pueblo Rico, 1584 m, the Paratype locality, on the road to Santa Cecilia. 4, Chocó, San José del Palmar, 1000 m on the Pacific slope in cloud forest. 5, Valle, Rio Bravo (upper Calima) in premontane and montane cloud forest. 6, Valle, Cerro los Chancos, near Calima Lake, 1600 m, in montane cloud forest. 7, Valle, Rio San Juan, km 56 near Queremal, 1200 m, in montane cloud forest.

the hindwing which resemble *P. hypaesia*, there is no evidence of a mimetic association between the two species. The two are parapatric, *P. mimica* occurring on the west slope and *P. hypaesia* on the east slope of the western cordillera. The genera *Dulcedo*, *Paradulcedo*, and *Pseudohaetera* are monotypic, with the latter two restricted to cloud-forest relicts in the Andean mountains. Lowland rain-forests are the province of the other neotropical Haeterini, *Cithaerias*, *Haetera*, and *Pierella*, with the greatest diversity in the Amazon Basin.

The restriction of haeterine adults to the deep shade of the forest understory (commonly undisturbed rain forests) renders them highly vulnerable to habitat disturbance. Most adults tend to stay within a confined area in the forest at all times. Adults cannot tolerate direct sunlight, and once forests are cleared the species disappear from their natural habitat. In secondary forests, haeterine species are seen rarely or are absent. As a result, *P. mimica* is seriously threatened as most of its natural habitats have been taken over for agriculture and pastures.

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THE *BEBEARIA MARDANIA* COMPLEX (NYMPHALIDAE)

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ABSTRACT. Six species are recognized in the African *Bebearia mardania* complex: *B. mardania* (Fabricius); *B. senegalensis* (Herrich-Schaeffer), **stat. rev.**; *B. theognis* (Hewitson), **stat. rev.**; *B. guineensis* (Felder & Felder), **stat. rev.**; *B. orientis* (Karsch); and *B. badiana* (Rebel), **stat. rev.** *Bebearia cocalia* (Fabricius) is placed as a synonym of *B. mardania* and the type-locality of both taxa, described from “Indiis,” is interpreted as Sierra Leone, West Africa. *Bebearia cocalioides* Hecq is newly placed as a subspecies of *B. mardania*, whilst *katera* (van Someren) (= *insularis* Schultze, **syn. nov.**; = *continentalis* Hecq, **syn. nov.**) is newly placed as a subspecies of *B. senegalensis*. The taxon *paludicola* (Schultze) is placed as a **new synonym** of *B. guineensis*, and both *dealbata* (Carcasson) and *taveta* Clifton are newly placed as subspecies of *B. badiana*. The identities of the various species and subspecies are discussed, and lectotypes are designated for *B. guineensis* and *B. badiana*.

Additional key words: Africa, taxonomy, lectotype designations, Fabrician species, type-localities.

Taxonomically, the *Bebearia mardania* complex is perhaps one of the most confused groups of African Nymphalidae. The identity of *B. mardania* (Fabricius) itself has been misinterpreted consistently ever since its original description nearly 200 years ago (Fabricius 1793). As generally recognized prior to Hecq (1988), the taxon actually comprised three distinct species—*B. mardania*, *B. senegalensis* (Herrich-Schaeffer) and *B. guineensis* (Felder & Felder). The two former taxa usually were regarded as subspecies, whilst *B. guineensis* has been lost in synonymy since Aurivillius (1899), following Butler (1871), incorrectly regarded it as the male of *B. mardania*. *Bebearia cocalia* (Fabricius) had been regarded variously as a form of *B. mardania*, as a monotypic species, or as a bitypic species that also included *B. theognis* (Hewitson). Hecq (1988) regarded *B. mardania* as a senior synonym of *B. theognis* and accepted *B. cocalia* as a separate, polytypic species. Actually, *B. cocalia* is the male of *B. mardania* and neither taxon has anything to do with *B. theognis*. The taxon *B. orientis* (Karsch) generally was regarded as a subspecies of *B. mardania* until its specific identity was recognized by van Son (1979). *Bebearia badiana* (Rebel) also generally has been regarded as a subspecies of *B. mardania* but two subspecies here transferred to it, *dealbata* (Carcasson) and *taveta* Clifton, were placed in a separate species, *B. dealbata*, by D’Abrera (1980). *Bebearia orientis* and *B. badiana* actually appear to be most closely related to *B. senegalensis*, the three forming an allopatric group. Possibly con-

¹ Present address: 5 Bogong Street, Riverhills, 4074, Brisbane, Queensland, Australia.

specific, they are regarded as separate species here for reasons discussed below.

It has not been practicable, nor indeed possible, to examine the relevant type material. The holotypes of *B. mardania* and *B. cocalia* were stated to be in the Drury Collection and are now believed lost. Syntypes of *B. senegalensis* are believed to have been in the Staudinger Collection but enquiries to Berlin failed to locate them; their present whereabouts, if still extant, are unknown to me. The types of forms *paludicola* Schultze and *insularis* Schultze also are believed lost. Fortunately, the types of *B. mardania* and *B. cocalia* were figured in William Jones' unpublished *Icones*, now preserved at the University of Oxford, while those of *B. senegalensis* were figured by Herrich-Schaeffer (1858). Syntypes of *B. orientis* and its synonym *pseudocalia* Staudinger are in the Zoologisches Museum der Humboldt Universität zu Berlin and color slides of these have been examined. Since this is the only species occurring in coastal East Africa, its identity is not in doubt. Holotypes of subspecies *dealbata* and *taveta* are in the National Museum of Kenya and both were adequately illustrated in the original publications (Carcasson 1958, D'Abrera 1980). Syntypes of *B. badiana* are in the Naturhistorisches Museum, Vienna, and color photographs of these have been examined. Holotypes of *B. cocalia continentalis* Hecq and *B. cocalioides* Hecq are in the Musée Royal de l'Afrique Centrale, Tervuren, and both have been figured (Hecq 1988). Holotypes or syntypes of the remaining taxa, *B. theognis*, *B. guineensis*, *B. mardania katera* (van Someren), and *B. orientis insularis* Kielland, are in The Natural History Museum, London. Apart from *B. guineensis*, of which color slides of the syntypes have been examined, these taxa had their types illustrated in the original publications (Hewitson 1864, van Someren 1939, Kielland 1985).

Fortunately, the available published and unpublished illustrations are sufficient to enable identification of the various species and subspecies and no problems remain that require a closer examination of types or topotypical material for their resolution. These, and material in the Natural History Museum of Zimbabwe, have enabled the complexities of this group to be resolved.

ABBREVIATIONS

The following abbreviations of Museums and collections are used throughout: BMNH—The Natural History Museum, London; NHMZ—Natural History Museum of Zimbabwe, Bulawayo; NHMV—Naturhistorisches Museum, Vienna; ZMHU—Zoologisches Museum der Humboldt Universität, Berlin; HCO—Hope Entomological Collections,

University of Oxford; BWC—B. Wilson Collection, Bulawayo; AHC—A. Heath Collection, Cape Town.

SYSTEMATICS

Family Nymphalidae Genus *Bebearia* Hemming *mardania* complex

Species in this complex are distinguished by the presence of a dark postdiscal band running across both fore- and hindwings on the underside. The complex is considered here to comprise six species, best identified by comparison with the figures and diagnostic notes provided. The following key is intended merely as a guide to identification, particularly in the case of females. Subspecies are distinguished primarily by female pattern characteristics. Where known, the larvae feed on palms (Palmae).

Carcasson (1981) considered *Bebearia* to be a subgenus of *Euphaedra* Hübner but provided no evidence for this reassignment. In the absence of revisionary studies on the genera in question, I prefer to maintain the traditional separation of *Bebearia* as a distinct genus.

Key to Species in the *mardania* Complex

- | | |
|--|---------------------|
| 1. Males | 2 |
| 1'. Females | 7 |
| 2. Forewing with a faint brown subapical bar but no yellow markings; hindwing rounded (Fig. 7); valvae elongate, with one long apical tooth and several broad subapical dentations (Fig. 20) | <i>theognis</i> |
| 2'. Forewing with at least a trace of yellow subapical markings; hindwing at least slightly angled; valvae not as above | 3 |
| 3. Forewing with a broad, distinct, yellow subapical bar; black apical area without a purplish suffusion; valvae short and apically rounded (Fig. 21) | <i>guineensis</i> |
| 3'. Forewing rarely with the yellow subapical bar broad and distinct; black apical area with a purplish suffusion; valvae elongate and apically produced or toothed | 4 |
| 4. Hindwing slightly angled (Figs. 3, 5); valvae with apex broad (Fig. 18) | <i>mardania</i> |
| 4'. Hindwing distinctly angled (Figs. 6, 8–10); valvae with apex narrowed (Figs. 19, 22, 23) | 5 |
| 5. Reddish above; upperside of hindwing with submarginal pale spots pronounced; valvae elongate and strongly produced apically into a dentate process (Fig. 22) | <i>orientis</i> |
| 5'. Purple to reddish-purple above; upperside of hindwing with submarginal pale spots not evident; valvae not as above | 6 |
| 6. Valvae broad, with several small apical teeth (Fig. 23) | <i>badiana</i> |
| 6'. Valvae elongate and slightly produced to a blunt point apically (Fig. 19) | <i>senegalensis</i> |
| 7. Hindwing rounded, not distinctly angled (Figs. 14, 15); forewing with subapical pale bar broad, not narrowing noticeably posteriorly; ground color brown to greyish-brown | 8 |
| 7'. Hindwing angled (Figs. 11–13, 16, 17); forewing with subapical pale bar narrow | |

- or narrowing noticeably posteriorly; ground color generally orange-brown to red-brown 9
8. Forewing subapical pale bar white *guineensis*
- 8'. Forewing subapical pale bar mostly yellow *theognis*
9. Forewing reddish-brown basal to subapical pale bar; submarginal pale spots generally diffuse and indistinct 10
- 9'. Forewing with a black area basal to subapical pale bar; submarginal pale spots generally distinct 11
10. Postdiscal areas paler than basal areas, often whitish; hindwing weakly angled (Fig. 11); forewing subapical pale bar white *mardania*
- 10'. Postdiscal areas not noticeably paler than basal areas; hindwing distinctly angled (Fig. 17); forewing subapical pale bar white or orange *badiana*
11. Hindwing with pale areas distad of submarginal dark line distinct; forewing with submarginal pale spot in space CuA_2 entirely orange *orientis*
- 11'. Hindwing with pale areas distad of submarginal dark line indistinct; forewing with submarginal pale spot in space CuA_2 partly or entirely white *senegalensis*

Bebearia mardania (Fabricius)

(Figs. 1–5, 11, 18)

Papilio mardania Fabricius, 1793:249 (♀). Type-locality “Indiis,” recte [Sierra Leone]; Jones’ Icones 3:70, fig. 1.

Papilio cocalia Fabricius, 1793:250 (♂). Type-locality “Indiis,” recte [Sierra Leone]; Jones’ Icones 3:70, fig. 2.

Nymphalis cocalia, Donovan, 1800–04:[53] (♂), pl. [36], fig. 1.

Euryphene senegalensis, Aurivillius, 1912:177, partim (♀) (Sierra Leone). Misidentification.

Najas cocalia theognis, Fox, 1965:229 (Liberia); Owen & Owen, 1973:597 (Sierra Leone). Misidentifications.

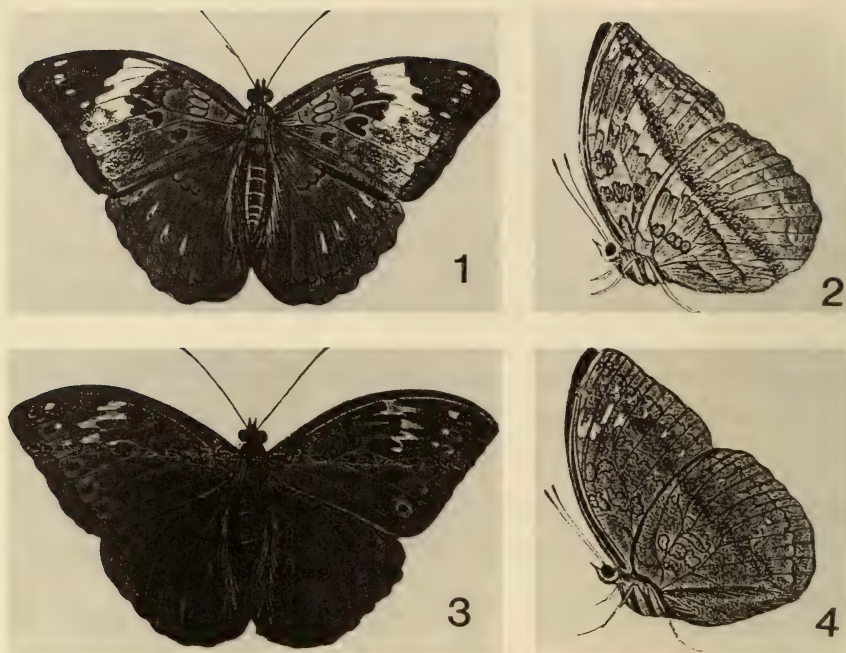
Bebearia cocalia, D’Abrera, 1980:309, partim (♂, 3rd ♀ only) (Kumasi, Ghana); Hecq, 1988:120 (♂ partim).

Bebearia mardania, Hecq, 1988:120 (♀ partim).

Diagnosis. The weakly angled hindwings in both sexes, pale postdiscal areas in the female, and shape of the valvae in the male, serve to distinguish this species. The typical subspecies differs from the next in having the female smaller and with a better developed subapical pale band on the forewing.

Discussion. Although Butler (1871) misinterpreted this species, his actions in placing *B. cocalia* as a synonym of *B. mardania* may be construed as that of first reviser, giving priority to the name *mardania*. This synonymy has been largely overlooked in subsequent publications. The name *mardania* has not been applied correctly since its original description but the figures in Jones’ Icones are accurate and enable this species to be interpreted correctly. Hecq (1988) referred to both these figures but associated the female (*mardania*) with male *B. theognis* and the male (*cocalia*) with female *B. senegalensis*.

It is probable that both taxa originated from the same source, since both were described from the Drury Collection at the same time from the same incorrect locality. Specimens agreeing well with both figures



FIGS. 1-4. Illustrations of Fabrician types in Jones' unpublished Icones, Vol. 3: Upper- and undersides of *Bebearia* species. 1 and 2, *B. mardania*, female. 3 and 4, *B. cocalia*, male (=synonym of *B. mardania*).

in Jones' Icones have been collected together near Abidjan in Ivory Coast and there can be no justification for continuing to regard *mardania* and *cocalia* as anything other than female and male respectively of the same nominal species.

Type-locality. Both *mardania* and *cocalia* were described originally from "Indiis" (India) but this is erroneous. The figures of both taxa in Jones' Icones closely resemble specimens from West Africa. Aurivillius (1899) mentioned only Cameroon for *cocalia* and this has been assumed to be its type-locality. However, specimens from there differ from typical specimens (as figured by Jones), and Sierra Leone is interpreted here as the type-locality for both taxa. It is known from historical records that ships en route to Europe from India stopped in this area to collect water and other provisions, and that Drury obtained material from this region.

Material examined. IVORY COAST: 3 ♂, 3 ♀, Azegny Nat. Park, W of Abidjan, x.1985 (NHMZ, BWC); 1♀, Abidjan, x-xi.1974 (NHMZ).

Distribution. Sierra Leone, Liberia, Ivory Coast, Ghana.

***Bebearia mardania cocalioides* Hecq, stat. rev.**

Euryphene cocalia, Aurivillius, 1899:198 (Cameroon); 1912:pl. 40 (♀). Misidentification.

Euryphene mardania ♀ f. *cocalia*, Peters, 1952:62. Misidentification.

Euphaedra cocalia, Fox, 1968:1266 (Congo); Carcasson, 1981:165. Misidentifications.

Bebearia cocalia, D'Abrera, 1980:309, partim (2nd ♀ only) (Cameroon). Misidentification.

Bebearia mardania, Berger, 1981:149, partim (♂ f. *cocalia*, ♀ f. *senegalensis*), pl. 119, figs.

1 (♂), 10 (♀) (Zaire). Misidentification.

Bebearia cocalioides Hecq, 1988:124, figs. 19, 20 (♂ ♀). Type-locality Eala, Zaire.

Diagnosis. The female tends to be larger and has the subapical white band of the forewing narrower and more deeply indented, particularly on its basal side, than in typical *mardania*.

Discussion. These Central African populations appear to represent a subspecies of *B. mardania* rather than a separate species. Males have not been available for genitalia dissection but both taxa agree in wing shape and male pattern; females of both also have pale postdiscal areas on the wings. Berger (1981) stated that the types of *B. badiana* were identical to this taxon but this is not the case. Most references to *B. cocalia* in the literature actually belong here.

Distribution. Cameroon, Congo, Zaire, Central African Republic.

***Bebearia senegalensis* (Herrich-Schaeffer), stat. rev.**

(Figs. 12, 19)

Euryphene senegalensis Herrich-Schaeffer, 1858:54, figs. 95–98 (♂ ♀). Type-locality Senegal.

Euryphene senegalensis, Aurivillius, 1899:198; 1912:177, partim (♂) (Senegal).

Euryphene mardania, Aurivillius, 1912:pl. 40 (♀ only). Misidentification.

Euryphene mardania senegalensis, Peters, 1952:62.

Najas mardania senegalensis, Fox, 1965:230 (Liberia & Guinea).

Najas mardania, Owen & Owen, 1973:598 (Sierra Leone). Misidentification.

Bebearia cocalia, D'Abrera, 1980:309, partim (1st ♀ only) (Enuchi, Ghana); Hecq, 1988:

120 (♂ partim, ♀) (Sierra Leone & Ivory Coast). Misidentifications.

Bebearia mardania senegalensis, D'Abrera, 1980:310.

Euphaedra mardania senegalensis, Carcasson, 1981:165.

Bebearia cocalia senegalensis, Hecq, 1988:121.

Diagnosis. The male has hindwings more angular than *B. mardania* but can be distinguished with certainty from *B. badiana* only by the more elongate, apically produced valvae. The female resembles that of *B. orientis* but differs in characters noted in the key. In the typical subspecies the female is a little variable in the extent of the reddish-brown areas, particularly on the forewing, but may be identified readily by the submarginal ring-shaped spot in space CuA₂ of the forewing, which is white on both its inner and outer edges.

Discussion. Although generally regarded as the western subspecies of *B. mardania*, this species is distinct and occurs sympatrically with the former. *Bebearia cocalia* of Hecq (1988) is essentially this taxon.

Its identity has been obscured by a lack of understanding of the true nature of *B. mardania*.

Material examined. IVORY COAST: 2 ♂, 8 ♀, Azegny Nat. Park, W of Abidjan, x.1985 (NHMZ & BWC).

Distribution. Senegal, Guinea Bissau, Sierra Leone, Guinea, Liberia, Ivory Coast, Ghana.

***Bebearia senegalensis katera* (van Someren), stat. rev.**

(Figs. 6, 13)

Euryphene guineensis, Felder & Felder, 1867:430, partim (♀) (Calabar, Nigeria). Misidentification.

Euryphene mardania, Butler, 1871:74, partim (♀), pl. 28, fig. 6 (♀) (Fantee, Ghana); Aurivillius, 1891:210 (Cameroon & Gabon); 1899:198, partim; 1905:4 (pupa); 1912:177, partim, pl. 40 (♂ only); Neave, 1910:37 (Lualaba, Zaire); Holland, 1920:187 (Zaire). Misidentifications.

Euryphene cocalia, Staudinger, 1885–86:148, pl. 52 (♂ ♀) (Cameroon, Gabon & Congo). Misidentification.

Euryphene senegalensis, Aurivillius, 1912:pl. 40 (♂ ♀). Misidentification.

Euryphene mardania var. *insularis* Schultze, 1920:721 (♀). Type-localities Santa Isabel & San Carlos, Fernando Poo (described as ♀ form, i.e., infrasubspecific). **Syn. nov.**

Euryphene mardania katera van Someren, 1939:52, pl. 14, figs. 3, 4, pl. 15, figs. 3, 4 (♂ ♀). Type-locality Katera, SW Uganda.

Euryphene mardania katera, Peters, 1952:62.

Najas mardania, Carcasson, 1966:24, 58, fig. 21 (W Tanzania & N Zambia). Misidentification.

Euphaedra mardania, Fox, 1968:1266, partim (Congo); Carcasson, 1981:46, partim (♀ only) (Zaire), 165; Dowsett, 1983:61, partim (below Nyika, NE Zambia). Misidentifications.

Bebearia mardania, Cornes, Riley & St. Leger, 1973:13; Larsen, Riley & Cornes, 1980:16 (Nigeria); D'Abreia, 1980:310, partim (♀ only); Berger, 1981:149, partim, pl. 119, figs. 5, 6 (♂), 9 (♀). Misidentifications.

Bebearia cocalia guineensis, Hecq, 1988:121, partim (♀). Misidentification.

Bebearia cocalia continentalis Hecq, 1988:122, figs. 3–6, partim (♂ only). Type-locality Beni, Zaire. **Syn. nov.**

Bebearia cocalia katera, Hecq, 1988:123; Kielland, 1990:118, pl. 36.

Bebearia orientis, Kielland, 1990:118, partim, pl. 36 (♀) (Tukuyu, SW Tanzania). Misidentification.

Diagnosis. The female of this subspecies differs from typical *senegalensis* in having the pale submarginal ring-shaped spot in space CuA₂ of the forewing mostly orange, with white scales only on its outer portion, in being generally orange-brown in ground color, and with the black apical area of the forewing well developed. The male valvae are identical to those of the typical subspecies. There is some variation in the width of the pale subapical forewing band in both sexes. Some males approach *B. guineensis* in the width of this band but the apical area has a purplish suffusion, the hindwing is more distinctly angled, and the valvae differ.

Discussion. The majority of references to *B. mardania* in the literature actually refer to this taxon. Hecq's (1988) subspecies *continentalis*

is a mixture of this taxon and *B. guineensis* (the female); the range of material available does not support its separation from *katera*. The female form *insularis* was stated by Schultze (1920) to have the wings darker basally than in mainland examples of *katera* but Hecq (1988), while not actually assigning the name to any particular taxon, noted that it was without value.

Although described (in a footnote) by Schultze (1920) as a variety of *B. mardania*, the name *insularis* was considered by him to apply only to females, in the sense of a form-name, and not to males also recorded from Fernando Poo (=Bioko). Thus the name is considered here to be infrasubspecific, under the provisions of Article 45 (g) (ii) (1) of the International Code of Zoological Nomenclature (1985). Nomenclatural problems would arise if this name, unmentioned in the literature between its original proposal and Hecq (1988), were to be regarded as valid at the subspecies level. It would become a senior synonym of *katera* and would result in *B. orientis insularis* Kielland becoming a homonym.

Material examined. NIGERIA: 1 ♀ (paralectotype of *E. guineensis* C. & R. Felder), labelled Calabar Type/ Felder Colln./ syntype (BMNH: color slides); 1 ♀, Ajessor-Ikom, ii.1958 (NHMZ); 2 ♂, 1 ♀, Ikom, iii.1956 & ix.1959 (NHMZ); CAMEROON: 1 ♀, Lomie, 6.viii.1962 (NHMZ); 1 ♀, Kumba Gorge, 19.ix.1962 (NHMZ); CENTRAL AFRICAN REPUBLIC: 1 ♀, Bangui, ii.1967 (NHMZ); ZAIRE: 1 ♂, 1 ♀, Sandoa, ii.1930 (NHMZ); 1 ♀, no locality, 1947 (NHMZ); 1 ♂, Kafakumba, x.1931 (NHMZ); 1 ♂, Kanzonze, Katanga, 20.ii.1968 (NHMZ); UGANDA: 4 ♂, Katera, Sango Bay, vi.1938 & xi.1953 (NHMZ); 1 ♂, Budongo Forest, 10.ii.1939 (NHMZ); ZAMBIA: 6 ♂, 1 ♀, Ikelenge, viii-ix.1961, 28.iv.1963, v.1964, 28.iv.1972, 7 & 20.v.1983 (NHMZ); 4 ♂, 4 ♀, Kashiba, Mpongwe, 5.v.1974 (NHMZ & AHC); 1 ♀, Chambezi R., x.1898-i.1899 (HCO: color slides).

Distribution. Ghana, Nigeria, Cameroon, Equatorial Guinea (Fernando Poo), Congo, Gabon, Central African Republic, Zaire, W Uganda, W Tanzania, N Zambia.

***Bebearia theognis* (Hewitson), stat. rev.**

(Figs. 7, 14, 20)

Euryphene theognis Hewitson, 1864:[41], pl. [21], figs. 3, 4 (♂). Type-locality Ashanti, Ghana.

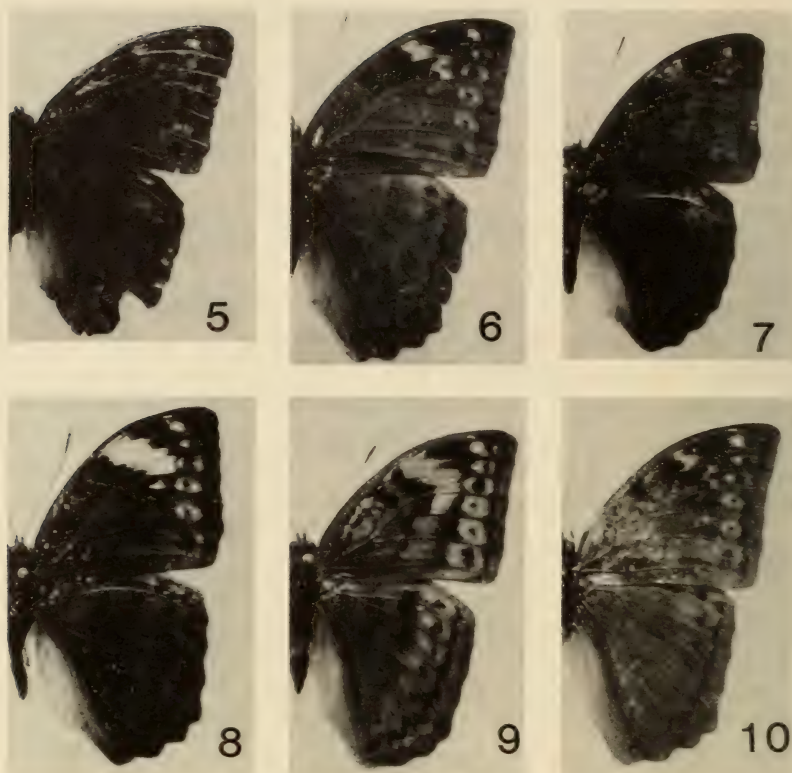
Euryphene theognis, Aurivillius, 1899:198; 1912:177, pl. 40 (♂ ♀); Peters, 1952:62.

Bebearia theognis, Cornes, Riley & St. Leger, 1973:13; Larsen, Riley & Cornes, 1980:16 (Nigeria); D'Abbrera, 1980:310, partim (♂ only).

Euphaedra cocalia theognis, Carcasson, 1981:165.

Bebearia mardania, Hecq, 1988:120 (♀ partim, ♂) (Ghana & Nigeria). Misidentification.

Diagnosis. The male is easily identified by its rounded hindwings,



FIGS. 5-10. *Bebearia* species, males. 5, *B. m. mardania*. 6, *B. senegalensis katera*. 7, *B. theognis*. 8, *B. guineensis*. 9, *B. o. orientis*. 10, *B. b. badiana*.

lack of yellow subapical markings on the forewing, and by the distinctive valvae. The female resembles that of *B. guineensis* in having rounded hindwings and a broad pale subapical band on the forewing, but may be readily differentiated by the yellow coloration in this band.

Discussion. This is the most distinctive species in the complex and Carcasson (1981) was incorrect in placing it as a subspecies of *B. cocalia* (= *mardania*), as the distinctive male valvae readily show. Hecq (1988) regarded *B. theognis* as a synonym of *B. mardania* but this is based on an incorrect interpretation of both the latter species and *B. cocalia*. It appears to replace *B. mardania* from Ghana to Nigeria and may be responsible for the disjunct distribution seen in that species.

Material examined. GHANA: 2 ♂, Takoradi, 24.xii.1939 (NHMZ); TOGO: 1 ♂, Amezdofe-Vane, 2300', xi-xii.1932 (NHMZ); NIGERIA: 4 ♂, 1 ♀, Lagos, iv.1955 (NHMZ); 2 ♂, 1 ♀, Ubiaja, Benin Province, vi & vii.1955 (NHMZ).

Distribution. Ghana, Togo, Nigeria.

***Bebearia guineensis* (Felder & Felder), stat. rev.**

(Figs. 8, 15, 21)

Euryphene guineensis Felder & Felder, 1867:430, partim (♂ only). Type-locality Calabar, Nigeria.

Euryphene mardania, Butler, 1871:74, partim, pl. 28 (♂ only) (Fantee, Ghana); Aurivillius, 1899:198, partim; 1912:177, partim; Peters, 1952:62. Misidentifications.

Euryphene guineensis, Aurivillius, 1891:210 (♂) (Cameroon).

Euryphene mardania ab. *paludicola* Schultze, 1920:721 (♀). Type-locality N'ginda, S. Cameroon. **Syn. nov.**

Euryphene mardania ♀ f. *paludicola*, Peters, 1952:62.

Euphaedra mardania, Fox, 1968:1266, partim (Congo); Carcasson, 1981:46, partim (♂ only) (Cameroon). Misidentifications.

Bebearia theognis, D'Abrera, 1980:310, partim (♀ only) (Kumasi, Ghana). Misidentification.

Bebearia mardania, D'Abrera, 1980:310, partim (♂ only); Berger, 1981:149, partim (♂ f. *mardania*), pl. 119, figs. 3, 4 (♂) (Zaire). Misidentifications.

Bebearia cocalia guineensis, Hecq, 1988:121, partim (♂).

Bebearia cocalia continentalis, Hecq, 1988:122, partim (♀ only) (Beni, Zaire). Misidentification.

Diagnosis. The male is easily recognized by the well marked, broad yellow subapical band on the forewing and by the lack of a purplish suffusion to the black apical area. The valvae are shorter than in the other species and the hindwing is a little less angled than in *B. senegalensis*, *B. badiana*, and *B. orientis*. The female resembles that of *B. theognis* in having the hindwing not distinctly angled, but has the subapical band of the forewing white without any yellow coloration.

Discussion. This species had been lost in the synonymy of *B. mardania* since Aurivillius (1899) until resurrected as a subspecies of *B. cocalia* by Hecq (1988). The shorter male valvae show it to be distinct. It is sympatric with *B. mardania*, *B. senegalensis*, and *B. theognis*. Felder and Felder's (1867) original material included a male of this species and a female of *B. senegalensis katera*; this incorrect association of the sexes was maintained by Hecq (1988). The description of form *paludicola* by Schultze (1920) is very brief, but sufficient to identify it as a female of this species, particularly as he noted its similarity to the female of *B. theognis* in a footnote. The female of *B. cocalia continentalis* (Hecq 1988) also belongs here.

Material examined. NIGERIA: Lectotype ♂, labelled Calabar vetus, Type/ guineensis n./ Felder Colln./ Syntype, here designated (BMNH: color slides); 2 ♂, 1 ♀, Ajessor-Ikom, ii.1958 (NHMZ); 1 ♀, Ikom, iii.1956 (NHMZ); 1 ♂, Mamu Forest, Awka, Onitha Province, iv.1960 (NHMZ); 2 ♂, Ayangba, Benin State (AHC); CONGO: 1 ♂, Mbe, 1-10.i.1974 (NHMZ); 1 ♂, Etoumbi Forest, ix-x.1960 (NHMZ); ANGOLA: 1 ♂, Lucala R., 228 km E of Luanda, 6.x.1964 (NHMZ).

Distribution. Ghana, Nigeria, Cameroon, Gabon, Congo, W Zaire, Angola.

Bebearia orientis (Karsch)

(Figs. 9, 16, 22)

- Euryphene senegalensis*, Oberthür, 1878:28; Holland, 1896:752. Misidentifications.
Euryphene orientis Karsch, 1895:277 (♂ ♀). Type-locality Dar-es-Salaam, Tanzania.
Euryphene senegalensis pseudocalia Staudinger, 1896:369 (♂ ♀). Type-localities Usagara & Lindi, Tanzania.
Euryphene senegalensis orientis, Neave, 1910:37 (lower Luangwa Valley, Zambia); van Someren, 1939:48, pl. 12, 13 (E. Kenya).
Euryphene mardania orientis, Peters, 1952:62.
Bebearia senegalensis orientis, Pinhey, 1965:92, pl. 19.
Bebearia mardania orientis, Pennington, 1978:70, pl. 88, 89; D'Abrera, 1980:310.
Bebearia orientis, van Son, 1979:117, pl. 13, Kielland, 1985:271; 1990:118.
Euphaedra mardania orientis, Carcasson, 1981:165.
Euphaedra mardania, Dowsett, 1983:61, partim (Malawi). Misidentification.
Bebearia cocalia orientis, Hecq, 1988:123.

Diagnosis. The pattern characters noted in the key, particularly the submarginal coloration on the hindwings in both sexes, enable identification of this species. The male valvae also are distinctive.

Discussion. Often regarded as a subspecies of *B. mardania* or *B. senegalensis*, the different shape of the male valvae and pattern details support the recognition of this taxon at the species level, as suggested by van Son (1979). The female from Tukuyu, SW Tanzania recorded by Kielland (1990) appears to belong to *B. senegalensis katera*.

Material examined. TANZANIA: 1 ♀ (syntype of *E. orientis*), labelled Dar-es-Salaam, Deutsch O.-Africa, 1895-7, v. Brgsn./ Deutsch Ost-Africa, 89-90, Richelm./ Origin. (ZMHU: color slides); 1 ♂ (syntype of *E. pseudocalia*), labelled Lindi, Deutsch Ost-Africa, 92-93, Knchhr./ Origin. (ZMHU: color slides); ZAMBIA: 1 ♂, Luangwa R., 13.x.1904 (HCO: color slides). Also 38 ♂ ♂, 22 ♀ ♀, from: KENYA: Mombasa; TANZANIA: Mukenge (Rufiji, Ulanga dist.); MALAWI: Mulanje, Zomba, Cholo, Mkuwadzi Forest; MOZAMBIQUE: Dondo Forest, Beira, Inhaminga; ZIMBABWE: Dichwe Forest (near Manghura), Honde Valley, Mutare, Vumba, Umvumvumu R. (near Chimanimani), Mt. Selinda (all NHMZ).

Distribution. S Somalia, E Kenya, E Tanzania, Mozambique, S Malawi, E Zambia, N & E Zimbabwe.

Bebearia orientis insularis Kielland

- Bebearia orientis insularis* Kielland, 1985:271, 272, figs. 1-4 (♂ ♀); 1990:118, pl. 36. Type-locality Ngezi Forest, Pemba Is., Tanzania.
Bebearia cocalia insularis, Hecq, 1988:123.

Diagnosis. The male has the subapical band of the forewing generally wider than in the typical subspecies. The female has the ground color brownish rather than reddish-brown in the basal half, whilst the distal half is pale ochraceous, paler than in typical *orientis*.

Distribution. Pemba Island, Tanzania.



11



12



13



14



15



16



17

FIGS. 11-17. *Bebearia* species, females. 11, *B. m. mardania*. 12, *B. s. senegalensis*. 13, *B. s. katera*. 14, *B. theognis*. 15, *B. guineensis*. 16, *B. o. orientis*. 17, *B. b. badiana*.

***Bebearia badiana* (Rebel), stat. rev.**

(Figs. 10, 17, 23)

Euryphene badiana Rebel, 1914:245 (♂ ♀). Type-locality Rutshuru, NE Zaire.*Euryphene mardania badiata*, van Someren, 1939:52, pl. 14, 15 (♂ ♀); Carcasson, 1958:9.

Incorrect subsequent spelling.

Euryphene mardania badiana, Peters, 1952:62.*Bebearia mardania badiana*, D'Abrera, 1980:310.*Euphaedra mardania badiana*, Carcasson, 1981:165.*Bebearia cocalia badiana*, Hecq, 1988:122.

Diagnosis. Similar in general appearance to *B. mardania* but both sexes have a more angular hindwing. Males can be separated with confidence from *B. senegalensis* only by the shape of the valvae.

Discussion. The broader male valvae and more extensive brown areas on the female suggest that this species is distinct from the closely related *B. senegalensis* and *B. orientis*, two species with more elongate and apically produced valvae and females that appear to mimic the common form of *Danaus chrysippus* (Linnaeus). Since *B. orientis* currently is accepted as a distinct species, it follows that *B. badiana* also must be regarded as a separate species.

Material examined. ZAIRE: Lectotype ♂, labelled *Euryphene badiana* Rbl. Type ♂ / Kutshuru Ebene [*sic*], 1400–1600 m, vi.1910, Grauer, here designated; Paralectotype ♀, same data but labelled Type ♀ (both NHMV: color photographs); UGANDA: 4 ♂, 1 ♀, Mbale, xii.1949 (NHMZ); 1 ♂, 1 ♀, Entebbe, v.1952 & x.1961 (NHMZ); 2 ♂, Tororo Forest, 29.vii.1965 & 1.viii.1966 (NHMZ); KENYA: 2 ♀, Kakamega Forest, 29–30.vii.1965 (NHMZ).

Distribution. NE Zaire, Uganda, W Kenya.

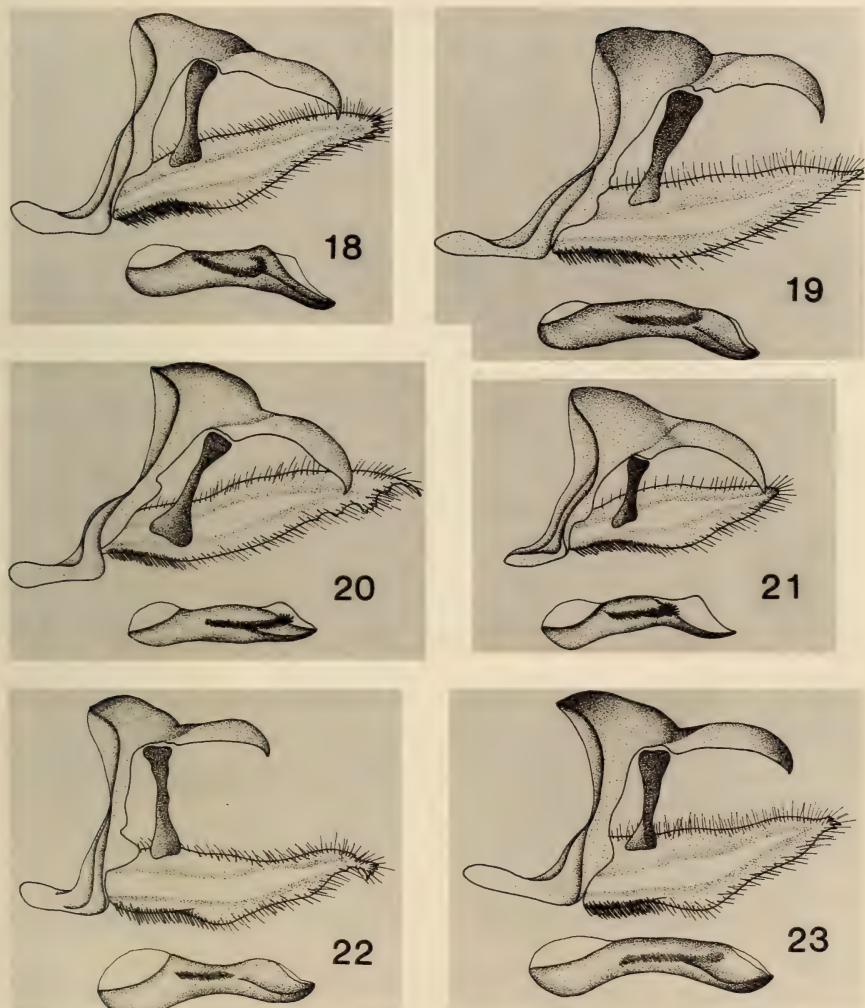
Bebearia badiana dealbata* (Carcasson), stat. rev.Euryphene mardania dealbata* Carcasson, 1958:8, figs. e, f (♂ ♀). Type-locality Mikinduri, Meru, E Kenya.*Bebearia dealbata dealbata*, D'Abrera, 1980:310.*Euphaedra mardania dealbata*, Carcasson, 1981:165.*Bebearia cocalia dealbata*, Hecq, 1988:123.

Diagnosis. The female differs from that of typical *badiana* in having the pale subapical band of the forewing yellowish orange rather than white. This band is also more or less horizontal towards the costa.

Distribution. East-central Kenya.

Bebearia badiana taveta* Clifton, stat. rev.Bebearia dealbata taveta* Clifton, in D'Abrera, 1980:310 (♂ ♀). Type-locality Taveta, S Kenya.*Euphaedra mardania taveta*, Carcasson, 1981:188.

Diagnosis. The female differs from that of typical *badiana* in the



FIGS. 18-23. *Bebearia* species, lateral view of aedeagus and male genitalia with left valvae removed. 18, *B. m. mardania*. 19, *B. s. senegalensis*. 20, *B. theognis*. 21, *B. guineensis*. 22, *B. o. orientis*. 23, *B. b. badiana*.

more orange ground color and in the white subapical band of the forewing being more or less horizontal towards the costa. This band is narrower than in subspecies *dealbata*.

Material examined. KENYA: 1 ♀, Tauta, v.1891 (NHMZ).

Distribution. South-central Kenya.

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GENERAL NOTES

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BIOLOGY OF *OPOSTEGOIDES SCIOTERMA* (OPOSTEGIDAE) IN OREGON

Additional key words: *Ribes hurtellum*, gooseberry, cambium miner, *Spizella passerina*, dung mimicry.

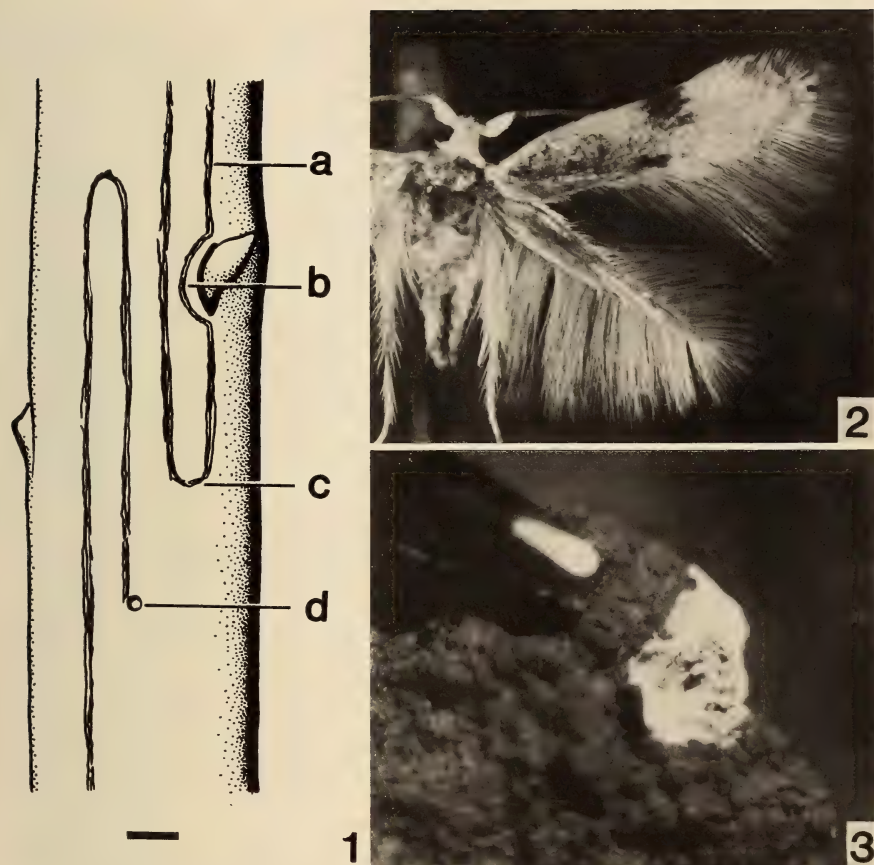
Although the Opostegidae are nearly world-wide in distribution (absent only in Arctic regions), the biology of the family is poorly known (Davis 1989). From 1956 to 1975 I had the opportunity to study *Opostegoides scioterma* (Meyrick) (Opostegidae) in the Willamette Valley of Oregon, where larvae of this species were found mining in the branch cambium of *Ribes hurtellum* (Michaux) (Gossulariaceae), a commercially grown gooseberry. Gooseberry cambium injury in Oregon has been reported previously by Rosenstiel (1960) and Eyer (1963).

Injury to gooseberry by opostegid larvae was first reported from New York by Grossenbacher (1910), who concluded that the cambium miner (*Opostegoides nonstrigella* Chambers = *O. scioterma*; D. R. Davis pers. comm.) "afforded entrance" to fungi which in turn "kill gooseberry shoots." Secondary invasion by fungi has not been observed in Oregon. Grossenbacher (1910) reported that *O. scioterma* also attacked red or garden currant (*Ribes vulgare* Lam.), as well as other species of *Ribes*, including European gooseberry (*Ribes grossularia* L.).

During my studies in Oregon, I never observed larvae of *O. scioterma* until mid-September because the minute size and translucent body color of early instars combine to make them virtually undetectable. By August, however, the thread-like prognathous larvae could be observed with a dissecting microscope by peeling away the bark of infested host branches (Fig. 1). The location of larvae within an infested branch was indicated by a line of darker green tissue above the mine, which contrasted with the light apple-green inner bark layer. By October, the larvae were half grown—0.5 mm wide and 3 mm long. Their thorax and abdomen were translucent; their mouthparts and cranial endoskeleton were pale tan. Each larva overwintered within its mine and resumed feeding in the spring. By late May larvae were full grown—approximately 0.6 mm wide and 11 mm long. Last instar larvae were similar in color and shape to early instar larvae. In early June, each larva made an enlargement 1.25 mm wide and 7 mm long at the terminus of its mine, which usually was located in the lower third of the branch. After forming this chamber, in which no frass was ever observed, larvae shed their penultimate skin. Next they cut a circular exit hole 1.25 mm wide in the bark of the host, emerged through the hole, and descended to the ground. Each larva penetrated the ground and formed a gray, roughly oval-shaped cocoon, 3–5 mm long. The cocoon was loosely covered with strands of silk and entangled with bits of debris so that it was highly cryptic. Pupae were tan, 1.5 mm wide, 2.5 mm long, oval in outline, and elliptical in cross section; they resembled flax seeds. The pupal stage lasted from late May until late June, which roughly corresponds with observations by Grossenbacher (1910).

Uniform soil samples (40 cm²) were taken on 10 June 1958 from beneath 12 infested plants to determine the depth of pupation. Samples from three successive depths (i.e., 0–2.5 cm, 2.5–5.0 cm, and 5.0–7.5 cm) were held in cloth cages in a greenhouse at summer temperatures. Emerging moths were counted at daily intervals. Of the 20 moths recovered during the period 18 June to 5 July, 60% came from the 0–2.5 cm soil depth, 19% from the 2.5–5.0 cm depth, and 14% from 5.0–7.5 cm depth. Wild moths emerged in the field from mid-June to the first week of July.

Larvae of *O. scioterma* injure gooseberry plants by destroying xylem cells during their cambium mining activities. Each bilateral mine is made by a single larva tunneling up and then back down a branch of the host (Fig. 1a). The parallel tunnels of each bilateral mine are uniformly 4–5 mm apart and joined at the top and bottom in an elliptical half



FIGS. 1-3. *Opostegoides scioterma* (Meyrick). 1, Sketch of larval mines in cambium; scale line = 10 mm (see text for explanation); 2, Adult with wings spread, dorsal aspect; 3, Bird dung deposit on dirt clod.

circle (Fig. 1c). An exception is observed occasionally when larvae mine partly around the base of a branch (Fig. 1b). In two-year-old infested plants, the injury causes leaves to wilt on the terminal 150-200 cm of the branches. By that time (usually May), 3-6 bilateral mines may be present in each branch.

In December 1958, the mean length of mine injury in two-year-old plants was 25 cm ($n = 70$) in branches 360 cm long. In that sample, 2-3 larvae were found per branch. Infested branches of four-year-old plants had 8-12 mines and branches were half their normal size. In two- to four-year-old infested plants, the old black frass in the mines was replaced in 10-20% of the mines by adventitious white cell tissue. About 10% of observed larvae mined in such tissue for 5-10 cm and then moved into normal cambium. This phenomenon also was noted by Grossenbacher (1910). Interruption of nutrient conduction due to mining activities curtailed fruit production, forcing growers to remove infested three-year-old plants just when the plants were reaching fruit-bearing stage. Following the infestation of older plants, gooseberry fields usually continued production for about 20 years.

The adult of *Opostegoides scioterma* is a small moth, with a wing span of about 8 mm and a large, white, feathery eyecap (Fig. 2). The forewing is white, with black dorsal spots, smaller dark costal spots, and a diffuse dark apical patch. The apex, termen, and dorsum of the forewing, and both margins of the hindwing have fringes of long white scales (Fig. 2).

During June and July when ambient temperatures are high, the moths remained sedentary on the tops of dirt clods in the gooseberry fields, with their wings spread flat against the substrate. Only physical disturbance caused them to move. For example, when a moth's abdomen was pushed with a pencil, the moth would run quickly 2–5 cm into a dark crevice in the soil or between clods and stop abruptly. After 5–10 seconds, it would return to its original position and resume its stationary posture.

Adults of *Opostegoides scioterma* exhibited a crepuscular activity pattern. At about 1800 h, 5–10% of the moths began their evening activities by making darting flights of 10–20 cm in many directions, moving from clod to clod, with 1–2-minute stops between flights. As daylight decreased, moths increased the frequency and distance of their flights. By 1900 h, 50–70% of the moths were flying, 30–60 cm at a time, with short rests between quick flights; most flights were toward gooseberry bushes. By 1930 h, flights were longer and generally ended in shaded central parts of the bushes where the moths alternated running and resting for 5–10 seconds among the inner branches. At about 2000 h, activity decreased, and by 2015 h, it had ceased for the night. Neither mating nor oviposition were observed.

During the day the small white moths were fairly conspicuous as they rested on dirt clods. However, they were not attacked by chipping sparrows [*Spizella passerina* (Beckstein); Fringillidae], which foraged in flocks for unharvested gooseberries in the same fields used by the moths. The sparrows habitually defecated on the tops of the same dirt clods upon which the moths rested during the day (Fig. 3). Resting moths, with their wings spread, were about the same size (8 mm diameter) and color (white with black dots) as the splashed bird droppings. The moths were present on about 20% of the clods where the sparrows defecated. Other species of birds were uncommon in the infested fields. The sparrows seemed oblivious to the resting moths, which may be avoiding detection by potential predators such as birds through "dung mimicry" (Endler 1981).

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REDESCRIPTION OF *PROTOLEURON RHODOGASTER* (SPHINGIDAE),
AN UNCOMMON NEOTROPICAL MOTH

Additional key words: Ecuador, Peru, taxonomy, *Aleuron*, *Stolidoptera*.

Protoleuron Rothschild and Jordan is a monotypic genus considered to be most closely related to *Aleuron* Boisduval and *Stolidoptera* Rothschild and Jordan (Rothschild & Jordan 1903, D'Abbrera 1986:104). *Protoleuron* shares with *Aleuron* the characteristic angular labial palpus; it is similar to *Stolidoptera* in its absence of a produced lobe at the anal margin of the hindwing and in the presence of symmetrical male genitalia. *Protoleuron* is distinguished from these two genera by the prominent, elongate, uniserial spines on the posterior abdominal tergites (Rothschild & Jordan 1903). *Protoleuron* is similar to *Stolidoptera* in wing maculation and coloration, but the lateral wing margin of the male forewing is distinctly dentate in *Protoleuron*, whereas it is more produced and scalloped in *Stolidoptera*.

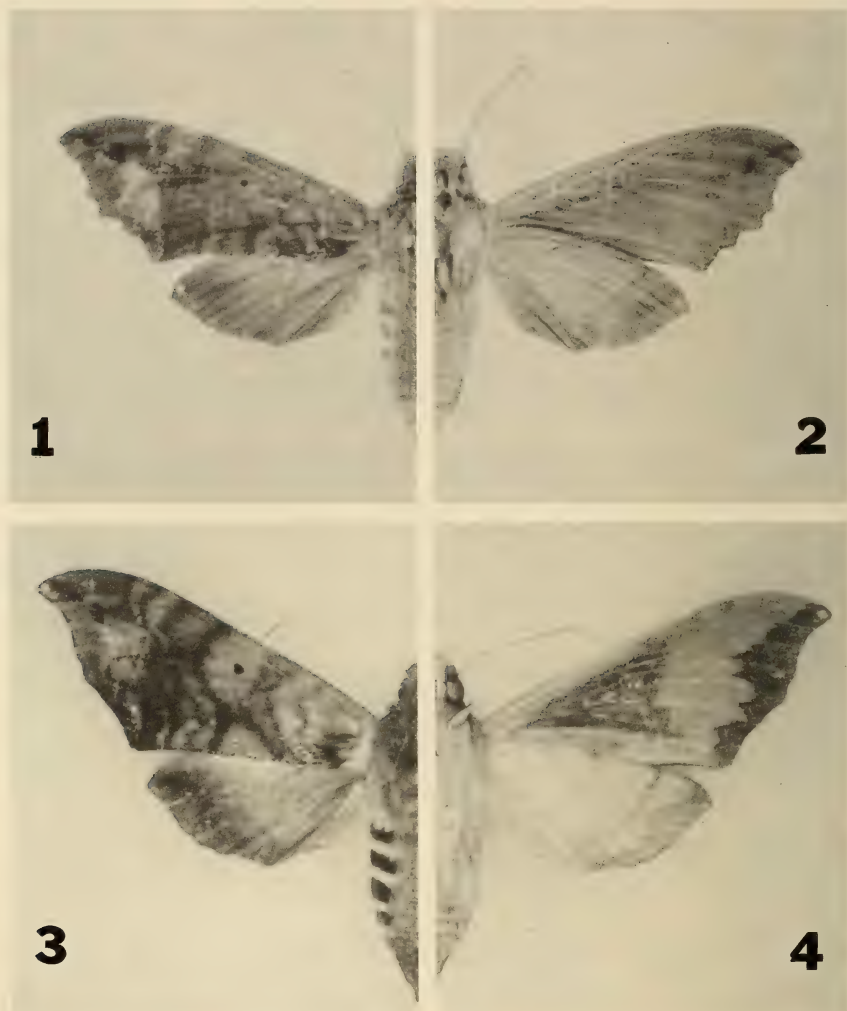
Apparently restricted to South America (Rothschild & Jordan 1903), *Protoleuron* is known from only two specimens—the holotype male from Ecuador and a female from Peru. The geographical range of *Stolidoptera* is reportedly broader—Mexico to Venezuela (D'Abbrera 1986:102). Here we report the capture of a third specimen of *Protoleuron rhodogaster* Rothschild and Jordan in Ecuador, and redescribe this little-known species.

On 27 May 1976, NRV collected a single female of *P. rhodogaster* near Cosanga, Napo Province, Ecuador, 2150 m, in a swampy clearing of primary cloud forest at 1900 h. No additional individuals of this species were observed during subsequent evenings at this collecting site.

The female was kept alive and, on the following day, she deposited 10-12 spherical (1 mm), glossy—almost translucent—off-white eggs along with a few abdominal setae and scales in the collection box. No changes in egg color were observed, but three days later, black, sparsely setose larvae emerged. Although several potential food plants in the area were offered to the caterpillars, an appropriate larval host apparently was not found. Subsequent visits to the locality found the habitat destroyed and the area developed.

Because the three known specimens of *P. rhodogaster* differ in wing coloration, and because the illustration of the dorsal surface of the holotype male (Rothschild & Jordan 1903: pl. 5, fig. 18) is considerably darker and does not illustrate some critical characters, especially the pinkish crimson shading below, we redescribe *Protoleuron rhodogaster* here.

Male. Head: Grayish olive above, buff mixed with olive below. Labial palpi angulate, pinkish crimson proximad, shading to buff admixed with olive distad. Antennae approximately one-half forewing length, pinkish crimson to reddish coral above, devoid of scales below, but with fine sparse setae and buff club. **Thorax:** Grayish olive above, grayish olive to buff overlaid with pinkish crimson below. Legs smooth, grayish olive proximad, shading to buff distad; spurs on hindtibia shorter and separated by a setal tuft. **Abdomen:** Blackish brown above, etched posteriorly in buff, with a dark gray-olive middorsal line; sternites pinkish crimson etched posteriorly in grayish olive. **Forewing:** Upper surface grayish olive, with prominent darker bands: one basal, three medial, and three postmedial; a blackish brown spot near end cell; incomplete dark brown oblique lines extending from near apex at R_3 to M_2 - M_3 at end cell; few blue-white scales at base, along anal margin, across end cell, and especially along the distal margin of distal postmedian band extending from M_1 - M_2 to Cu_2 -2A. Lower surface olive brown in basal two-thirds, distal area overlaid with pinkish crimson to coral; incomplete dark brown oblique line enhanced below and coalesced with the distal postmedian band, the last deeply incised in M_1 - M_2 . Fringe dark gray-brown above and below. **Hindwing:** Upper surface dull gray-brown. Lower surface pinkish crimson in anterior two-thirds, shading to dull grayish olive posteriorly, with two or three subtle postmedian bands. Fringe dark gray-brown above, gray below.



FIGS. 1-4. The two known females of *Protoleuron rhodogaster*. 1-2, Peru (CMNH): 1, Dorsal aspect; 2, Ventral aspect. 3-4, Ecuador (collection of J. M. Cadiou): 3, Dorsal aspect; 4, Ventral aspect.

Female (Figs. 1-4). Similar to male, but differs in body coloration below, which in female is predominantly coral to crimson, particularly on the abdomen. **Forewing:** Upper surface markings more distinct than in male, especially the darker postmedian bands; the distal median and proximal postmedian bands coalesce in Cu_2-2A . Lower surface dark gray-brown, with the area distad of distal postmedian band lighter gray-brown, with sparse red-coral to crimson scales. Distal postmedian band not as deeply incised in M_1-M_2 as in male. **Hindwing:** Similar to male in coloration, but lighter in discal area.

The three known specimens of *Protoleuron rhodogaster* are: holotype male, Ecuador (Hope Entomological Collections, Oxford University); female (Figs. 1, 2), Peru (Carnegie

Museum of Natural History); and female (Figs. 3, 4), Ecuador, Napo, Cosanga, 2100 m, 27.v.1976, N. R. Venedictoff (private collection of J. M. Cadiou). Forewing lengths: holotype male, 37 mm; females, 33 mm and 44 mm.

The female of *Protoleuron rhodogaster* collected near Cosanga, Ecuador, is similar to the holotype male in coloration and wing maculation, but the pinkish crimson areas on the wings are considerably brighter. The antennae of this female were bright reddish coral initially and darkened slightly with age. In addition, the ventral body is overscaled much more heavily with reddish coral. The shape of the lateral wing margin is variable among the three specimens, but the marginal dentation is less distinct in the females.

Despite the variation in wing shape, wing maculation, and coloration of the ventral surface, this species is distinct and cannot be mistaken for any other neotropical sphingid. The unexpected time of capture (1900 h) may indicate an early flight time that might account for the infrequent collection of *Protoleuron rhodogaster*. We encourage other collectors to be more observant and adaptable in their field collecting schedules.

We thank David Spencer Smith, Hope Entomological Collections, for providing photographs of the type specimen; and Robert Davidson and John Rawlins, Section of Invertebrate Zoology, Carnegie Museum of Natural History, for the loan of the female specimen from Peru. We particularly thank J. M. Cadiou for sharing information and Lee D. Miller for comments on the manuscript.

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THREE NOMINAL GENERA OF CRAMBIDAE OMITTED FROM "THE GENERIC NAMES OF MOTHS OF THE WORLD, VOLUME 5, PYRALOIDEA"

Additional key words: Pyraustinae, Nymphulinae, *Arthromastix*, *Nothomastix*, *Microdracon*.

Warren (1890) formally described 19 new genera of Pyraloidea, and these have found their places in the literature of the group. However, within the descriptions of two of these genera he published three additional generic names that have been overlooked almost totally. These are *Arthromastix* Warren, *Nothomastix* Warren, and *Microdracon* Warren.

Arthromastix and *Nothomastix* were proposed in the diagnosis of *Pardomima* Warren (1890:478). According to Warren (1890), *Pardomima* is "Distinguished from *Arthromastix lauralis* (*Salbia lauralis* Guen.) and *Nothomastix chromalis* (*Botys chromalis* Wlk.), with which it otherwise agrees, by the simple male antennae and untufted legs." Though a common character is given to distinguish the two genera from *Pardomima*, this in itself does not qualify as a description or diagnosis as it does not distinguish them from each other. However, one previously published species is included in each (*Salbia lauralis* "A.

Guenée" [see Postscript below] for *Arthromastix* and *Botys chromalis* Walker for *Nothomastix*). This qualifies as an "indication" under Article 12(b)(5) of the Third Edition (1965) of the *International Code of Zoological Nomenclature*, and makes the names available, fixing the respective type species by monotypy. Fletcher and Nye (1984) omitted these names, though Martin (1955) cited them in his revision of African species of *Pardomima*. Both genera are valid and belong to the subfamily Pyraustinae and tribe Spilomelini. *Arthromastix* is Neotropical and contains only the type species, which was placed by Hampson (1899:655) in *Pilocrocis* Lederer, with its synonym *Ceratoclasia verecundalis* Berg, 1874. The latter is a **new combination** with *Arthromastix*. *Nothomastix*, on the other hand, is Indo-Australian. In addition to the type species, the following nominal species belong to *Nothomastix*: *Sylepta obliquifascialis* Hampson, 1896; *Notarcha pyranthes* Meyrick, 1894; *Conogethes sisyroptila* Meyrick, 1933 (according to Shaffer, *in litt.*, a synonym of *N. chromalis*, **new synonymy**); *Sylepta klossi* Rothschild, 1915; and *Botys pronaxalis* Walker, 1859 (= *Pardomima acutalis* Hampson, 1893). Partly following previous authors, Klima (1939) placed these additional species in *Syllepte* Hübner, 1823 (as *Sylepta* Hübner [1825]), except for *C. sisyroptila*, which he transferred to *Dichocrocis* Lederer. All of them form **new combinations** in *Nothomastix*.

The third genus, *Microdracon*, belonging to the subfamily Nymphulinae [**new sub-family placement**], presents a somewhat different case. Referring to his new genus *Opisthedeicta*, Warren (1890) wrote, "This genus is akin to the first division (A) of Snellen's *Oligostigma*, cf. Tijd. v. Ent. xix 1876, p. 189, for which I have proposed the generic term *Microdracon*. *Opisthedeicta*, however, is characterized by a peculiar formation . . . [etc.]" Hence, Warren (1890) (a) gave characters to differentiate *Microdracon* from *Opisthedeicta*; (b) gave "a bibliographic reference to a previously published description or definition," i.e., that given by Snellen (1876) for his Division A of *Oligostigma* Guenée; and (c) by implication included in *Microdracon* the two species placed by Snellen in that division, viz., *O. bilinealis* Snellen, 1876, from the Punjab, and *O. unilinealis* Snellen, 1876, from Java. Though these are not cited individually in Warren's paper, Snellen's tabulation is clear and unambiguous, and thus the two species are in Warren's paper "clearly referred to [*Microdracon*] by bibliographic reference." Therefore, though the diagnosis from the previously undescribed *Opisthedeicta* might be considered circular, the generic name is available by indication under both Article 12(b)(1) and Article 12(b)(5) of the International Code. From the two originally included species, I hereby designate *Oligostigma bilinealis* Snellen, 1876, as type species of *Microdracon* Warren, 1890 [**new designation**]. This will make *Microdracon* a subjective synonym of *Parapoynx* Hübner, [1865] 1816 [**new synonymy**], according to the classification of Yoshiyasu (1985, 1987), with which I agree.

Postscript. M. Shaffer (*in litt.*) notes, "One small problem needs bearing in mind about the validation of *Arthromastix*. Warren in 1890 incorrectly attributed the species *lauralis* to Guenée, the correct author being Walker. Martin in 1955 attributed the correct author to *lauralis*. As there is only one *Salbia lauralis*, we can therefore justify the assumption that Warren was referring to the same species, otherwise it could be argued that as there is no such species as *Salbia lauralis* Guenée, we cannot use the Article 12(b)(5) to indicate a species that does not exist." The reference for the original description of *Salbia lauralis* is Walker (1859). I agree that Warren clearly intended to designate Walker's species, and that his citation of Guenée as author was an inadvertent error. Under Article 67(f) of the International Code, Warren's designation of the type species is valid, even though as subsequent author he attributed its name "to an author or date other than that denoting its first establishment."

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PALATABILITY OF SEVEN BUTTERFLY SPECIES (NYMPHALIDAE) TO TWO TYRANT FLYCATCHERS IN BRAZIL

Additional key words: color patterns, Tyrannidae, foraging behavior, predators.

Palatability of butterflies to predators that hunt visually generally is related to patterns of coloration. Thus unpalatable species tend to have brightly colored wings that advertise to predators their distasteful properties, whereas palatable ones tend to be cryptic (Fisher 1930). In spite of recent investigations (Chai 1986), we estimate that only about 30 of the 3000 described species of Nymphalidae have been tested for palatability. Most previous studies focused on the palatability of temperate species to captive animals (almost always to birds and lizards). Few field data on the interactions between butterflies and predators have been reported (e.g., Brower 1984).

In this paper we investigate the palatability of free flying individuals of *Callicore astarte astarte* Cramer, *Catacore kolyma connectens* (Talbot), *Diaethria clymena clymena* (Cramer), *Pyrrhogyra neaerea arge* Gosse, *Marpesia norica* (Hewitson), *Marpesia chiron* (Fabricius), and *Temenis laothoe* (Cramer) (all Nymphalidae: Nymphaliinae) to wild individuals of two tyrant flycatchers, *Hirundinea ferruginea* Sclater and *Tyrannus melancholicus* Vieillot (Tyrannidae). The first three butterfly species exhibit warning coloration patterns (on the upper surface of the wings) when flying, with a predominance of red, black, blue, and yellow; such coloration suggests that they are unpalatable. The other four species (which do not exhibit such colors) were tested as controls.

Field work was conducted in July 1988 in the Serra dos Carajás (5°54'-6°33'S; 49°53'-50°34'W) in the southern portion of the State of Pará, Brazil. Butterflies were caught in lowland forest (Pojuca, <100 m elevation) characterized by *Mimosa* spp., grasses, and small patches of dry forest, and many tyrant flycatchers. Butterflies were released 10 to 30 m upwind of the birds, always near the end of the afternoon when the predators feed (Fitzpatrick 1980). Palatability tests with *H. ferruginea* were conducted using a single pair of birds near their nest site. A combination of different butterfly species was offered

TABLE 1. Responses of two wild tyrant flycatchers, *Hirundinea ferruginea* (H.f.) and *Tyrannus melancholicus* (T.m.), to seven species of free-flying butterflies (n = 63 individuals).

Butterfly	Bird	Observation from perch	Pursuing without capture	Capture and release	Capture and eating
<i>Callicore astarte</i>	H.f.	12	—	2	—
	T.m.	2	3	2	2
<i>Catacore kolya</i>	H.f.	1	—	—	—
	T.m.	2	—	—	—
<i>Diaethria clymena</i>	H.f.	5	1	—	—
	T.m.	1	1	1	1
<i>Pyrrhogyra neaerea</i>	H.f.	3	—	—	2
	T.m.	—	—	—	4
<i>Marpesia norica</i>	H.f.	—	—	—	3
	T.m.	1	—	—	5
<i>Marpesia chiron</i>	H.f.	—	—	—	1
<i>Temenis laothoe</i>	H.f.	—	—	—	8
Total		27	5	5	26

sequentially to the birds. In the case of *T. melancholicus*, the number of birds involved in the experiment was nearly the same as the number of butterflies offered (n = 25).

The birds' responses (Table 1) were pooled into four categories: (1) "Observation from perch," when a bird observed a butterfly and moved only its head. Butterflies that did not elicit this response were considered as not sighted by the birds. (2) "Pursuing without capture," when a bird flew near a butterfly for closer observation, but did not attempt to capture it. (3) "Capture and release," when a bird followed and captured a butterfly and released it afterwards. (4) "Capture and eating," when a butterfly was swallowed after capture. The first two responses were considered to be sight-rejection of the butterfly; the last two were considered to be taste-test in which butterflies were rejected (released) or accepted (eaten).

The response of the birds to butterflies offered are presented in Table 1. The brightly colored species *C. astarte*, *D. clymena*, and *C. kolya* were considerably less attractive to the birds than the other species. Of all individuals of these three species tested, 78% (n = 36) were rejected on sight by the birds, 14% were rejected after taste trials (especially *C. astarte* and *D. clymena*), and 8% were eaten. Butterflies rejected were released alive without apparent injury, as they flew to a safer place after release by birds.

Conversely, 85% (n = 27) of butterflies showing other color patterns (i.e., *M. norica*, *M. chiron*, *T. laothoe*, and *P. neaerea*) were attacked quickly by the birds and consumed (including the wings). *Pyrrhogyra neaerea* sometimes was sight-rejected by *H. ferruginea*, but it always was eaten by both bird species when captured.

Our palatability data agree with those described by Chai (1986) for *M. chiron*, *T. laothoe*, and many other species in the genera *Callicore*, *Diaethria*, *Marpesia*, and *Pyrrhogyra* that were tested with jacamars (*Galbula ruficauda*; Galbulidae). The unpalatability we found for *Callicore astarte* suggests that the similarities of color patterns among several species in this genus may be mimetic.

Individuals of *H. ferruginea* and *T. melancholicus* responded similarly in their acceptance and rejection of each butterfly species. Even so, there were slight differences: *H. ferruginea* rejected more butterflies on sight than *T. melancholicus*, which also captured and ate some of the butterflies considered unpalatable. Such differences may be

due to the more generalized habits of *T. melancholicus*, which is found in a greater variety of habitats and probably has a more generalized diet.

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AN OVERLOOKED RECORD OF *LACINIPOLIA RODORA* (NOCTUIDAE) FROM THE UNITED STATES

Additional key words: Mexico, national record, United States.

Lacinipolia rodora (Dyar) (Noctuidae) was described as *Polia rodora* Dyar (1911) from a single female from Mexico City, Mexico. The type specimen (Type No. 12958), collected by R. Mueller, is deposited in the collection of the United States National Museum (USNM), Smithsonian Institution, Washington, D.C. It has long been recognized by several noctuid workers that *Lacinipolia rodora* ranges into southwestern United States, but owing to unfortunate circumstances, this information has never been published in a formal manner.

In the early 1960's, Lloyd Martin began a taxonomic study of the genus *Lacinipolia* McDunnough, based primarily on material in the collection of the Natural History Museum of Los Angeles County (LACM). The subsequent loss of his notebook with photographs of all the type specimens and extensive descriptive notes, caused Martin to abandon his study. In 1975, Charles Selman completed a revision of *Lacinipolia* as his doctoral dissertation at Ohio State University. Selman's (1975) study was a complete taxonomic revision, including descriptions, photographs, and genitalic drawings. Due to the length of the document and unforeseen difficulties, Selman's dissertation was never published. Required copies of his dissertation were deposited in the library of Ohio State University. Photocopies have been made available, but minimal distribution of photocopies does not satisfy the requirements for formal publication as identified in the International Code of Zoological Nomenclature (Stoll et al. 1961).

Selman (1975) proposed the new combination *Lacinipolia rodora* in his dissertation,

hence, the new combination was never formally published. Poole (1989) implied that this new combination had been published by Godfrey (1972). In the paper to which Poole (1989) referred, Godfrey (1972:138) described the larvae of *Lacinipolia rodora* from ova secured by J. G. Franclemont in the Chiricahua Mountains of southeastern Arizona. Thus, the occurrence of *L. rodora* in the United States and the new combination were published together, although Godfrey was unaware that he created a new combination. Prior to Poole (1989), Godfrey's (1972) contribution apparently went unnoticed, since *L. rodora* was not included by Franclemont and Todd (1983) in the Check List of the Lepidoptera of America North of Mexico.

Lacinipolia rodora is similar to *L. vicina* (Grote), but can be distinguished from the latter by the presence of bipectinate male antennae; male antennae are serrate in *L. vicina*. A male specimen of *L. rodora* in the collection of the USNM with the same data as the female holotype was designated as the lectotype by Selman (1975). However, because the holotype is extant and the latter specimen was not mentioned by Dyar (1911), the lectotype designation is unnecessary and invalid; it also is unpublished.

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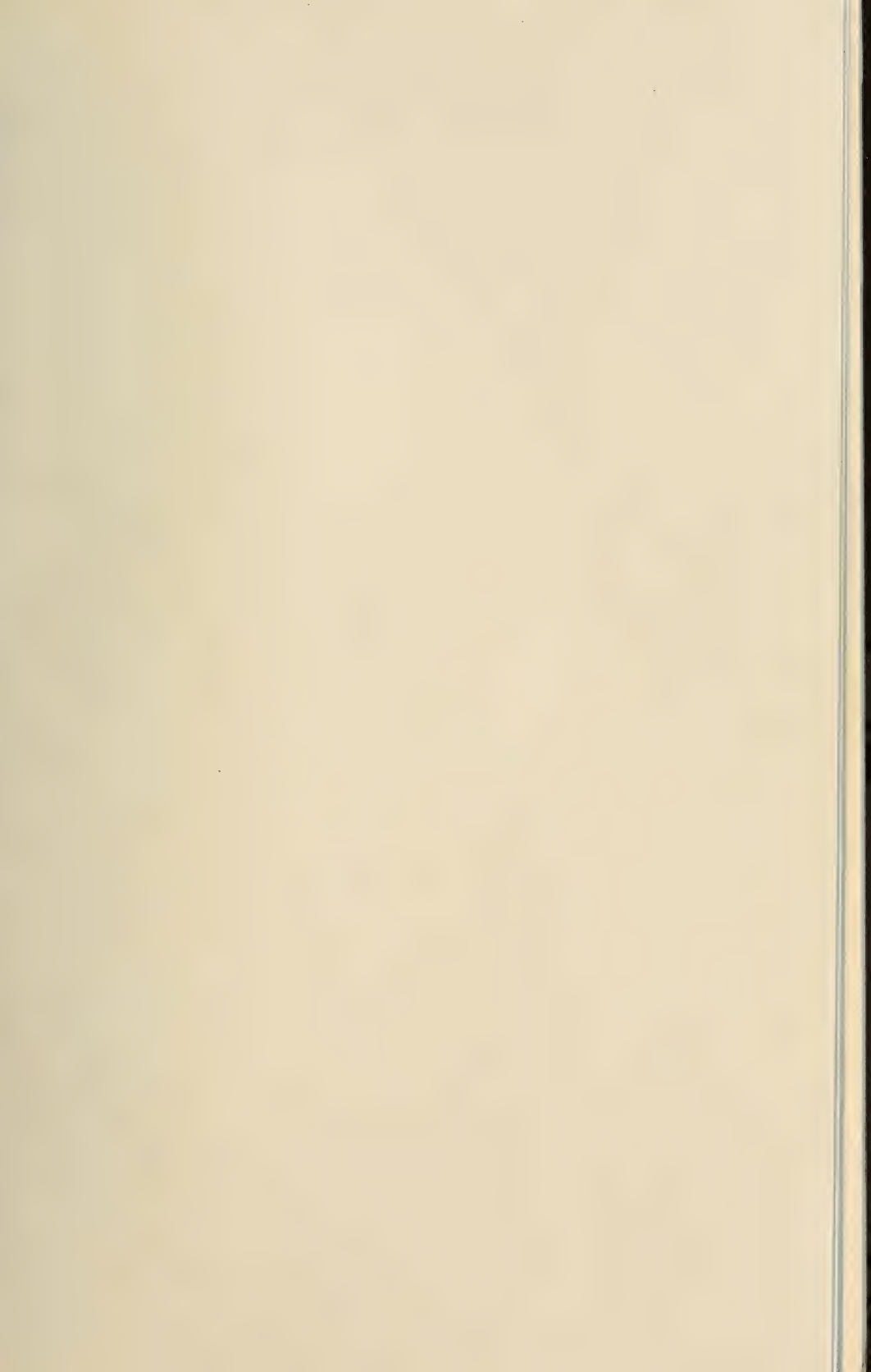
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CONTENTS

GENITALIC RECASTING OF <i>POANES</i> AND <i>PARATRYTONE</i> (HESPERIIDAE). <i>John M. Burns</i>	1
MALE MATE-LOCATING BEHAVIOR IN THE COMMON EGGFLY, <i>HYPOLIMNAS BOLINA</i> (NYMPHALIDAE). <i>Ronald L. Rutowski</i>	24
<i>COENOCHROA CHILENSIS</i> , A NEW PHYCITINE MOTH FROM CHILE (PYRALIDAE). <i>Jay C. Shaffer</i>	39
<i>PARADULCEDO</i> , A NEW GENUS OF SATYRINAE (NYMPHALIDAE) FROM WESTERN COLOMBIA. <i>Luis M. Constantino</i>	44
THE <i>BEBEARIA MARDANIA</i> COMPLEX (NYMPHALIDAE). <i>David L. Hancock</i>	54
GENERAL NOTES	
Biology of <i>Opostegoides scioterma</i> (Opostegidae) in Oregon. <i>R. G. Rosenstiel</i>	70
Redescription of <i>Protoleuron rhodogaster</i> (Sphingidae), an uncommon neotropical moth. <i>Jacqueline Y. Miller and Nadia R. Venedictoff</i>	73
Three nominal genera of Crambidae omitted from "The generic names of moths of the world, volume 5, Pyraloidea." <i>Eugene Munroe</i>	75
Palatability of seven butterfly species (Nymphalidae) to two tyrant flycatchers in Brazil. <i>C. E. G. Pinheiro and M. Martins</i>	77
An overlooked record of <i>Lacinipolia rodora</i> (Noctuidae) from the United States. <i>Ron Leuschner</i>	79
MANUSCRIPT REVIEWERS, 1991	81
ANNOUNCEMENT	
PUBLICATIONS OF THE LEPIDOPTERISTS' SOCIETY	82

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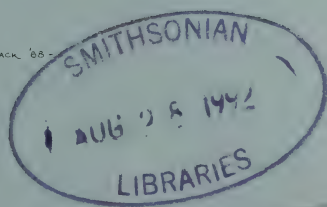
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Cover illustration: Male of the brightly-colored, day-flying buckmoth, *Hemileuca electra* Wright (Saturniidae). The larval host is flat-top buckwheat, *Eriogonum fasciculatum* Benthham (Polygonaceae). Submitted by Callie Mack, 8529 Jackie Drive, San Diego, California 92119 U.S.A.

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THE BUTTERFLIES OF ANAK KRAKATAU, INDONESIA: FAUNAL DEVELOPMENT IN EARLY SUCCESSION

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ABSTRACT. A survey in 1990 revealed that the butterfly fauna of Anak Krakatau continues to increase: of 41 species now recorded from this recent volcanic island, 18 have arrived since 1986. Habitat relations, faunal development, and the possible future of the island's butterflies are discussed. Continued vegetational succession is likely to result in extinction of a number of species, especially Hesperiidæ and Lycaenidæ, which depend on grassland or coastal low-growing vegetation formations.

Additional key words: Lepidoptera, conservation, island biogeography, vulcanism.

The pattern of colonization of the Krakatau Islands, Indonesia, by butterflies since the sterilizing eruption of 1883 was described by New et al. (1988) on data available to 1986. The island of Anak Krakatau, which emerged permanently from the sea only in 1930, is an active volcano and was devastated by eruptions in 1952 (when all vegetation was destroyed) and severely damaged by volcanic activity most recently in 1970-71. The island is of particular interest in studies of biotic colonization and community development as it provides one of very few isolated tropical sites in which such processes can be assessed from their earliest stages. Studies there of ecologically informative taxa and the progressive increase in species richness are useful in assessing the relationship between degree of habitat isolation and ability to recover from severe perturbation, a theme relevant to practical conservation. By 1985, 23 species of butterflies had been found on Anak Krakatau. Bush and Whittaker (1991) recorded an additional 13 species in 1989, and 5 more species are noted here from our visit in August/September 1990. Most of these 41 are likely to have arrived from the relatively close older islands of Rakata, Panjang, and Sertung, but other species are clearly from further afield. These are known from Java and Sumatra but not from elsewhere on the Krakatau.

This paper is an account of the butterfly fauna of Anak Krakatau in

1990, when the status and distribution of these insects were appraised in relation to the increasing complexity of this initially simple island environment. Background information on Anak Krakatau is included in Thornton and Rosengren (1988), and a broader picture of invertebrate colonization on the island is provided by Thornton and New (1988) and Thornton et al. (1990).

METHODS

During the period 19 August–3 September 1990, members of our group re-mapped the vegetation of Anak Krakatau to quantify changes in its composition and extent that had occurred during the previous five years. All vegetated areas were surveyed repeatedly for butterflies using three methods. 1. Transect walks (using the method of Pollard 1977) were made over all habitats at intervals during each of 11 days, with a minimum of 5 day-surveys in each. In each habitat, main comparisons are based on transects at 1030 h and 1400 h, but discrete counts were made at seven times on each of several days (Fig. 10), as time permitted. The butterflies were identified, counted and, where possible, sexed to yield data on species incidence, relative abundance in different vegetation types, and activity patterns. 2. Six selected taxa were marked on the hindwing underside using colored felt-tip pens (Pentel®), and released at the point of capture, in the air, within 10 minutes of capture. This technique was employed only in calm weather. Recaptures were used to detect any major individual movement. 3. Casual observations and collecting were undertaken during other work on all parts of the island. Data both from transect counts and recaptured marked butterflies were used to estimate relative abundance of species and their distribution among different vegetation types. The latter data are not strictly quantitative, as most species occurred in only small numbers. The following abundance categories are used for comparison between major habitats: (i) common, at least 10 individuals seen in a representative 100 m transect at some time between 1000 and 1600 h; (ii) moderately common, three to nine individuals seen on at least one transect during the above period; (iii) rare, fewer than three individuals seen on any transect and usually not present on all transects; (iv) singletons.

Status is appraised as follows: (i) resident, species associated with presence of larval foodplants, usually common or moderately common, with both sexes present and (for some) mating pairs observed, or for which any of these have been recorded in the past; (ii) non-resident, species which did not fulfill the above criteria and for which no known larval foodplants are present on Anak Krakatau; (iii) straggler, as non-

resident, but mainly strongly-flying migratory species that were either rare or singletons.

Vouchers of some taxa were taken for confirmation of identity, although singleton females and several easily-recognizable or strongly flying species (noted in the following list) were not captured. Hesperidae were identified by A. F. Atkins; members of other families were identified from standard literature (such as Corbet & Pendlebury 1978, and many of the papers cited therein) and by comparison with material captured earlier on the Krakatau. A few records were made during a brief visit by IWB and D. Britton in April 1991; those of significance are noted below. Vouchers of all Krakatau butterflies captured during our surveys are held at La Trobe University or the Zoological Museum, Bogor.

RESULTS AND DISCUSSION

Vegetation

Anak Krakatau (Fig. 1) is largely bare lava and ash, with well-defined vegetation on the eastern coastline extending up to about 200 m inland. The maximum extent of vegetation has increased substantially since 1986, and there have been marked changes in diversity and maturity. The three major areas, designated the Eastern Foreland, Northeast Headland, and Northern Foreland supported fairly discrete vegetational communities in 1986, and still were distinct sufficiently in character in September 1990 to be regarded as different habitats (as different successional stages), though by this time they were no longer separated by distinct vegetation-free areas. Succession is most advanced on the Eastern Foreland, where well-developed *Casuarina equisetifolia* J. R. & G. Forst (Casuarinaceae) woodland is becoming progressively invaded by other secondary forest species. Well defined grassland areas (*Ischaemum muticum* L.) and natural clearings between groups of trees also are present. In contrast, the youngest area, the Northern Foreland, has predominantly grassland (*Ischaemum muticum*, *Imperata cylindrica* (L.) Beauv., *Saccharum spontaneum* L., Gramineae) communities with younger *Casuarina* to the west. The vegetation of the Northeast Headland is intermediate between these two. There are numerous *Ficus* L. trees (Moraceae) toward the coast on the Northeast Headland and Eastern Foreland, and low vegetation (*Ipomoea pes-caprae* (L.) R. Br. (Convolvulaceae) communities, with *Canavalia maritima* (Aubl.) Urb. and other legumes) extends along much of the coast, but is least developed along about 200 m immediately south of the Northeast Headland.

Clumps of *Saccharum* and occasional small *Casuarina* trees occurring

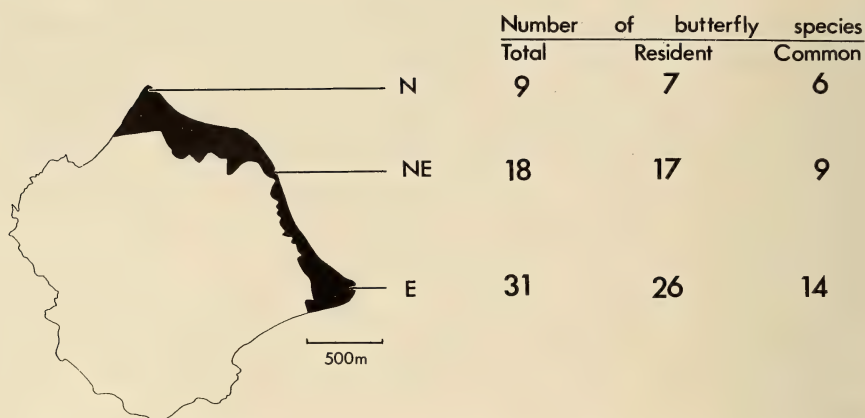


FIG. 1. Anak Krakatau, with summary of numbers of butterfly species found in each of three main vegetated areas in 1990. Extent of vegetation indicated by shading. (E, Eastern Foreland; NE, Northeast Headland; N, Northern Foreland.)

up much of the lower slope of the outer cone are not shown on the map in Figure 1.

Butterflies

Although collecting intensity differed between the three main areas, with most collecting in the more complex habitats of the Eastern Foreland, the surveys collectively included repeated collections over all vegetated areas of Anak Krakatau, so that few species flying at the time of our survey would have been missed, and inferences on distribution and relative abundance are reliable. The following annotated checklist of the species observed gives the year of first record on Anak Krakatau in parentheses and on the archipelago in brackets following the specific name (1982: Yukawa 1984; 1983: Bush 1986; 1984–85: New et al. 1988; 1989; Bush & Whittaker 1991; 1990: this paper).

Papilionidae

Graphium agamemnon (L.) (1984–85) [1982]. Two individuals sighted, both on 22.viii.90 on beachfront vegetation, Eastern Foreland; one resting on *Eupatorium odoratum* L. (Compositae) blossom. Status: straggler.

Graphium sarpedon (L.) (1990). One seen on 20.viii.90 near beach, Eastern Foreland. Not seen previously on the archipelago. Status: straggler.

Pachliopta aristolochiae (F.) (1984–85) [1919–21]. Both forms *adamus* and *antiphus* were seen frequently in treed areas and along woodland edges of the Eastern Foreland and Northeast Headland; seen rarely in the Northern Foreland. Present also iv.91. Status: resident.

Papilio memnon L. (1990) [1983]. One worn specimen seen on 23.viii.90 in the Eastern Foreland. Formerly recorded from Rakata and Sertung only. Status: ? straggler; could

possibly become resident soon, as suitable larval foodplants (Rutaceae) now occur on Anak Krakatau (T. Partomihardjo, pers. comm. 1990).

Troides helena (L.) (1989) [1908]. Moderately common in coastal forest and along woodland edges of the Eastern Foreland (where present also in iv.91); one seen on the Northeast Headland. Previously known from the other three islands. Status: resident, recently established.

Pieridae

Catopsilia pomona (F.) (1984–85) [1933]. Several individuals seen on beachside vegetation of the Northeast Headland and Eastern Foreland; one flying over bare lava in the southwest of the island, 21.viii.90. Status: migrant, ? non-resident.

Eurema blanda (Boisduval) (1983) [1919–21]. Not uncommon on coastal and other low vegetation in all areas; most frequent in the Eastern Foreland. Status: resident.

Eurema hecabe (L.) (1984–85) [1919–21]. Not as common as *E. blanda* and found only in the Eastern Foreland and Northeast Headland. Status: resident.

Nymphalidae

Danaus chrysippus bataviana Moore (1990) [1919–21]. One seen on 26.viii.90 in woodland clearing in Eastern Foreland. Known previously from Rakata and Sertung. Status: ? straggler.

Danaus genutia (Cramer) (1989) [1908]. Form *sumatrana* Moore was fairly common in clearings in the Eastern Foreland and Northeast Headland and a few individuals of form *intensa* Moore also were present. Status: resident.

Euploea modesta Butler (1989) [1908]. Individuals were seen nearly every day in the Eastern Foreland, more rarely on the Northeast Headland. First recorded from a single specimen (Bush & Whittaker 1991), and earlier records of *Euploea* sp. from Rakata and Sertung (New et al. 1988) may be of this species. Status: resident, recent colonist and apparently increasing in numbers. [D. Britton, pers. comm., captured a specimen in Northern Foreland in April 1991].

Ideopsis (Radena) juvena (Cramer) (1983) [1919–21]. Common in the Eastern Foreland and less so in the Northeast Headland, virtually ubiquitous in vegetated areas but most frequent in clearings and along woodland and coastal edges. (Seen also iv.91). Status: resident.

Tirumala septentrionis Butler (1989) [1983]. A single specimen found in a woodland clearing of the Eastern Foreland, 31.viii.90. Status: resident (Bush & Whittaker 1991). Known earlier (1983) from Rakata.

Melanitis leda (L.) (1982) [1933]. Not uncommon in all vegetated parts of the island and roosting under cliff overhangs along the coast southeast of the Eastern Foreland. Status: resident.

Mycalesis janardana Moore (1989) [1919–21]. Few individuals found in shaded clearings and open forest in the Eastern Foreland, more rarely in the Northeast Headland. It was found on all four islands in 1989 and known earlier (1982, of the more recent surveys) from Rakata and Sertung. Status: resident.

Orosotriaena medus (F.) (1983) [1919–21]. One individual seen on 31.viii.90 in the Eastern Foreland. Status: probable resident.

Neptis hylas (L.) (1984–85) [1908]. Not common, but a few individuals seen in both the Eastern Foreland and Northeast Headland. Status: resident.

Precis atlites (L.) (1984–85) [1983]. Not common, but seen daily from 26.viii.90 in open areas in all parts of the vegetated areas. Status: resident.

Precis sp. (?*palmana javana*) (1990). Identity not confirmed. A single specimen of a bright orange *Precis* was seen resting on *Saccharum* in E on 1.ix.90 (TRN), but evaded capture. It did not resemble any species earlier recorded from the archipelago, and TRN had little doubt of its identity: the species is widespread in Malaysia and Indonesia. Status: ? straggler.

Lycaenidae

Miletus symethus (Cramer) (1984-85) [1982]. Not common, but seen regularly in forested areas of the Eastern Foreland. Status: resident.

Catochrysops strabo (F.) (1982) [1933]. Common throughout the coastal vegetation and seen occasionally in grassland areas within the Eastern Foreland. Status: resident.

Euchrysops cnejus (F.) (1983) [1919-21]. Rare. Seen only in one clearing in the Eastern Foreland where it was present also in 1985 and 1986. Status: resident.

Jamides aratus (Stoll) (1984-85) [1982]. Infrequent and apparently restricted to coastal vegetation of the Eastern Foreland. Status: resident.

Jamides celeno (Cramer) (1982) [1919-21]. Much more common than *J. aratus* and found along most of the vegetated coastline. Status: resident.

Lampides boeticus (L.) (1982) [1933]. Not common, but widely distributed along the vegetated coastline. Status: uncertain, possible resident but population almost certainly augmented by migration.

Zizina otis lysizone (Snellen) (1982) [1982]. Common on coastal vegetation in Eastern Foreland, more rarely in other clearings and further north. Status: resident.

Zizula hylax (F.) (1984-85) [1982]. Common, but less so than *Z. otis*, and with similar distribution. Status: resident.

Arhopala pseudocentaurus (Doubleday) (1989) [1919-21]. Several individuals seen patrolling forest edges of the Eastern Foreland. Status: presumed resident and recent colonist from other islands.

Hypolycaena erylus (Godart) (1983) [1919-21]. Not common, but seen most days in forest clearings of the Eastern Foreland. Status: resident.

Hesperiidae

Potanthus confucius (C. & R. Felder) (1982) [1919-21]. (See comments on identity of this taxon in New et al. 1988). Abundant in grasslands in the Eastern Foreland; few seen in open areas of the Northeast Headland; occasional individuals in the Northern Foreland. Status: resident.

Polytremis lubricans (Herrich-Schaeffer) (1989) [1908]. Confirmed from Anak Krakatau by Bush and Whittaker (1991), with earlier record erroneous (New et al. 1988). Rare in open grassland and woodland clearings of the Eastern Foreland. Found on Rakata in 1908 and 1919-21, but not seen on the archipelago since then except on Anak Krakatau. Status: presumed resident.

Pelopidas conjunctus (Herrich-Schaeffer) (1990) [1919-21]. Rare in open grassland in the Eastern Foreland. Found on Rakata and Sertung prior to 1921 and on Rakata in 1933. Not seen on the archipelago since then, although Yukawa (1984) recorded a *Pelopidas* as ?*agna* (Moore) from Sertung. Status: presumed resident.

Previously Recorded Species Not Found in 1990

Danaus melanippus (Cramer) (1984-85) [1908]. Seen commonly in 1984-86, but not found in 1989 (Bush & Whittaker 1991) nor in 1990. Specimens from our earlier collections have been compared carefully with recently captured *D. genutia*, and differ clearly in identity. It is possible that *D. genutia* has now replaced *D. melanippus* on Anak Krakatau.

Hypolimnas anomala (Wallace) (1982) [1919-21]. Possibly a sporadic migrant rather than resident on Anak Krakatau.

Precis orithya L. (1989). Seen by Bush in 1989 and then new to the archipelago (Bush & Whittaker 1991).

Anthea emolus (Godart) (1989) [1984]. Previously known only from Rakata, and recorded from Sertung and Anak Krakatau in 1989 (Bush & Whittaker 1991).

Jamides bochus (Stoll) (1989) [1982]. Previously recorded from Sertung (Yukawa 1984) and recorded from Rakata and Anak Krakatau in 1989 (Bush & Whittaker 1991).

Borbo cinnara (Wallace) (1982) [1982]. Not found in 1989 or in 1990.

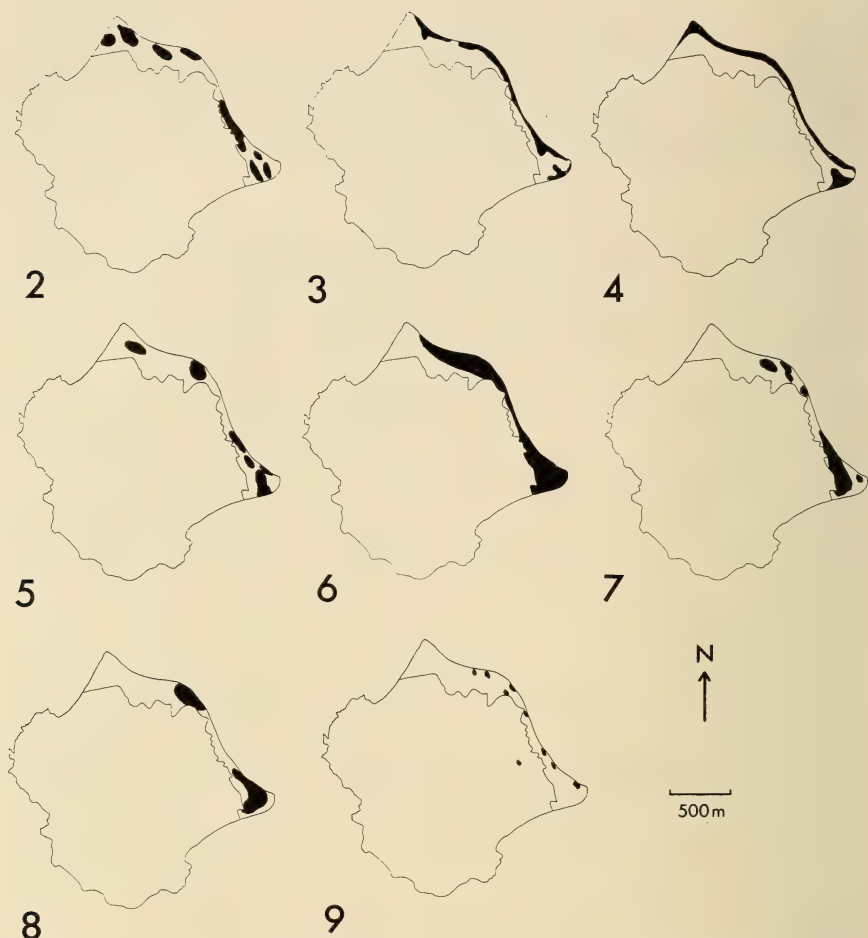
Hasora taminatus Huebner (1989). Recorded as new to the archipelago from Anak Krakatau in 1989 (Bush & Whittaker 1991).

Parnara cf. *guttatus* Bremner (1989). Also recorded as new to the archipelago from Anak Krakatau in 1989 (Bush & Whittaker 1991).

Telicota augias L. (1989) [1919–21]. The first record of the species on the archipelago since its occurrence on Rakata in 1919–21 (Bush & Whittaker 1991).

DISCUSSION

Forty-one species of butterfly have been recorded from Anak Krakatau (an increase of 18 since 1986), and up to about 30 of these are likely to be resident, some with populations augmented by regular migration. Only *C. pomona* has been observed migrating in the area by us, but the following species also are known migrants: *G. agamemnon*, *G. sarpedon*, *P. aristolochiae*, *E. hecabe*, *D. chrysippus*, *D. genutia*, *E. modesta*, *T. septentrionis*, *M. leda*, *P. atlites*, *L. boeticus*. Records of many of these are included in Williams (1930). Most species are clearly associated with the Eastern Foreland, fewer with the Northeast Headland, and fewest with the Northern Foreland (Fig. 1). All species of uncertain status in 1990 occurred in the Eastern Foreland, and no species were confined to the Northern Foreland. The general distributional picture is one of progressive attenuation both in species richness and overall abundance from the Eastern Foreland northward, corresponding to the less diverse vegetation structure and composition of other areas (Thornton & Rosengren 1988). About half the species recorded from each area were common there, but relative abundance in the areas differed (below). Distribution patterns of selected resident species are shown in Figs. 2–9. *Potanthus confucius* (Fig. 2) occurs in all grassland habitats on the island and was numerically the most abundant species during our survey. It was conspicuously more abundant in the Eastern Foreland (up to 14/100 m of grassland transect; mean of 26 transects between 0715 and 1730 h, 9/100 m) than in the Northeast (mean of 5.8/100 m in 14 transects) and in the Northeast than in the Northern Foreland (<2/100 m, 12 transects). It exemplifies well an impending slow expansion from a well-established population, largely dependent on *Ischaemum* (the larval food plant), in the Eastern Foreland and is a morning-active species (Fig. 10). As examples of the several widely distributed Lycaenidae associated with *Ipomea pes-caprae* formations, *Z. otis* (Fig. 3) and *C. strabo* (Fig. 4) both have coastal distributions; that of *C. strabo* is somewhat more extensive. Several residents appear to have wide but disjunct distributions on the island: *P. atlites* (Fig. 5) was found in all three main vegetated areas, but was not observed between these. In contrast, *R. juvena* (Fig. 6) was absent from the Northern Foreland but widely distributed elsewhere. *Euploea modesta* (Fig. 7) occurs in the more densely wooded areas and was not



FIGS. 2-9. Distribution (in black) of selected butterfly species on Anak Krakatau, 1990: 2, *Potanthus confucius*; 3, *Zizina otis*; 4, *Catochrysops strabo*; 5, *Precis atlites*; 6, *Radena juvena*; 7, *Euploea modesta*; 8, *Troides helena*; 9, *Catopsilia pomona*. Margin of vegetated area shown.

found in the Northern Foreland (but was present there by 1991), and the distribution of *T. helena* was generally similar (Fig. 8). In contrast to these residents, the incidence of the migrant *C. pomona* (Fig. 9) was very patchy, and a number of other migrants were seen only in the Eastern Foreland. All resident species (Table 1) occurred in the Eastern Foreland.

Many resident species are restricted in their distribution on Anak Krakatau; Table 1 ranks the more common species by relative abundance. The abundances of several species appear to have changed

TABLE 1. Relative abundance (1 = most abundant) of butterfly species in the three main habitat areas of Anak Krakatau, Aug.-Sept. 1990. Status of each species in each area shown as common (C), moderately common (MC), rare (R), as defined in text.

Sequence	Region		
	North	Northeast	East
1	<i>P. confucius</i> (R)	<i>C. strabo</i> (C)	<i>P. confucius</i> (C)
2	<i>Z. otis</i> (R)	<i>P. confucius</i> (MC)	<i>Z. otis</i> (C)
3	<i>E. blanda</i> (R)	<i>E. blanda</i> (MC)	<i>Z. hylas</i> (C)
4	<i>Z. hylas</i> (R)	<i>Z. hylas</i> (MC)	<i>C. strabo</i> (C)
5	<i>C. strabo</i> (R)	<i>Z. otis</i> (MC)	<i>E. blanda</i> (C)
6	<i>P. atlites</i> (R)	<i>P. aristolochiae</i> (MC)	<i>R. juvena</i> (C)

considerably since 1986, although the substantial natural fluctuations that can occur in insect populations imply the need for caution in this suggestion. The decline of *D. melanippus* is anomalous, but declines of several Lycaenidae (e.g., *Jamides*, *C. strabo*) may reflect some reduction of the extent of *Ipomoea pes-caprae* formations, especially around the southern part of the Eastern Foreland. Other taxa have remained remarkably constant. For example, it seems that the small colony of *E. cnejus* may have persisted without expansion of size or range since 1986. Some conspicuous recent colonizers, such as *T. helena* and *E. modesta*, have become very well-established within a short time.

As Bush et al. (1990) noted, butterfly assemblages on the Krakataus are strongly 'habitat-determined,' and the relatively early stage of succession on Anak Krakatau enables reliable correlation between resident butterflies and their preferred or obligate habitats. Anak Krakatau also is important in providing butterfly habitats not otherwise readily available on the archipelago. Several extinctions on the older islands in the 1920's, particularly of HesperIIDae, were attributed to forest closure eliminating grassland habitats (New et al. 1988). It is notable that three of those species, *T. augias*, *P. conjunctus*, and *P. lubricans*, that were not seen in the Anak Krakatau grasslands in 1984-86, and possibly others, have appeared recently in similar areas on Anak Krakatau after apparent absence from the archipelago of some 60 years. Their future on the island merits detailed appraisal to clarify the role of the island in the 'ecological rescue' (Thornton et al. 1990:152) of such early succession taxa whose habitats are declining elsewhere on the archipelago. The danaine *D. genutia sumatrana*, which inhabits *Casuarina* clearings, also now may be limited to Anak Krakatau. Another species, *C. panormus*, now persists only on the Sertung spit, which also supports *Casuarina* grassland; this species, too, should be studied in the future to determine whether or not it persists there.

The recent arrival on the archipelago (to Anak Krakatau) of two

TABLE 2. Incidence and relative abundance of resident Anak Krakatau butterflies in major vegetation types, Aug.-Sept. 1990. Vegetation types (1-6) are (1) *Ipomoea pes-caprae* associations, (2) *Ischaemum* grassland, (3) *Imperata*, *Saccharum* grassland, (4) *Casuarina*, (5) other woodland, (6) woodland clearings; — = absent, c = common, MC = moderately common, R = rare (see text); number in table list = more abundant species in each habitat from 1 (most abundant), down.

Species	Vegetation type					
	1	2	3	4	5	6
<i>P. aristolochiae</i>	—	R	R	5R	1MC	4MC
<i>T. helena</i>	—	—	—	R	4MC	MC
<i>E. blanda</i>	4MC	2MC	4MC	R	—	R
<i>E. hecabe</i>	MC	3R	MC	R	—	—
<i>D. genutia</i>	R	R	R	2MC	R	2MC
<i>E. modesta</i>	—	—	R	6R	2MC	R
<i>R. juvena</i>	6MC	R	R	1MC	3MC	1MC
<i>T. septentrionis</i>	—	—	—	—	—	R
<i>M. leda</i>	R	R	R	R	5MC	R
<i>M. janardana</i>	—	—	—	—	R	R
<i>O. medus</i>	—	R	—	—	—	—
<i>N. hylas</i>	R	—	—	R	R	R
<i>P. atlites</i>	R	R	R	R	R	MC
<i>M. symethus</i>	—	R	—	R	R	R
<i>C. strabo</i>	2C	4R	R	R	—	—
<i>E. cnejus</i>	—	—	—	—	—	R
<i>J. aratus</i>	R	R	—	—	—	—
<i>J. celeno</i>	5MC	R	2MC	R	—	—
<i>L. boeticus</i>	R	R	R	R	—	R
<i>Z. otis</i>	1C	R	3MC	3MC	—	R
<i>Z. hylas</i>	3C	R	—	—	—	R
<i>A. pseudocentaurus</i>	—	—	—	—	—	R
<i>H. erylus</i>	—	—	—	—	—	R
<i>P. confucius</i>	MC	1C	1MC	R	—	3MC
<i>P. lubricans</i>	—	R	R	—	—	R
<i>P. conjunctus</i>	—	R	R	—	—	—
Total resident species	14	18	15	16	10	20

hesperiids, *H. taminatus* and *P. guttatus*, and the nymphalid *P. orithya*, and (to the Sertung spit) of the lycaenids *Allotinus unicolor*, *Nacaduba beroe*, and *Prosotas lutea* illustrates the biogeographical roles that these two areas, both of which carry early vegetational stages, may play in permitting colonization of the archipelago by open country butterflies that would otherwise find no suitable habitat on the islands.

None of the species at present on Anak Krakatau can be considered a true 'forest butterfly.' Most are taxa associated with secondary or transitional seral stages, and are characterized by relatively good dispersal powers and broad geographical distributions. The most abundant species in each major habitat are listed in Table 2, and most of these are highly characteristic of the habitat noted. Butterfly species richness in grassland is rather similar to that on low coastal vegetation and also to open woodland and associated small clearings. However, closed wood-

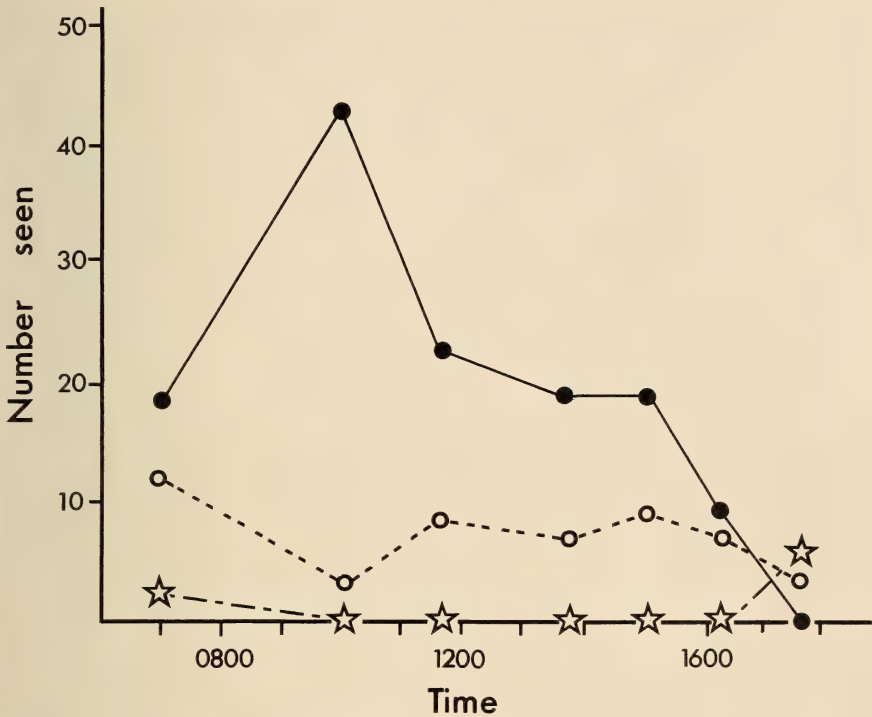


FIG. 10. Daily activity patterns of selected butterfly species on Anak Krakatau, based on transect walks. Solid circles: *Potanthus confucius*; open circles, *Radena juventa*; stars, *Melanitis leda*.

land-secondary forest has relatively few species associated with or restricted to it. Much of this limitation reflects availability of larval food-plants. As examples, New et al. (1988) emphasized the key nature of legume-dominated low coastal vegetation in promoting the establishment of many species on the Krakataus; Gramineae-dependent Hesperiiidae depend on stands of grasses with little over-story; and *Aristolochia* L. (Aristolochiaceae) vines are restricted largely to secondary forest areas in the Eastern Foreland, coinciding with the major distribution of consumers such as *T. helena* and *P. aristolochiae*. In woodlands, these two species and *E. modesta* were restricted almost completely to denser areas, but most others occurred more commonly along edges and in smaller clearings where sunlight could penetrate. The most common such species, *R. juventa*, flew throughout the day without any major activity peaks (Fig. 10), and *D. genutia* also was common. The Satyrinae are 'furtive' and occurred in long grass in shaded clearings. Several Lycaenidae (e.g., *A. pseudocentaurus*, *H. erylus*, *E. cnejus*) were found only along woodland edges.

There was little evidence of interchange or movement of butterflies between habitat patches. Recaptures were obtained for all of the species marked and released at their points of capture: *I. juventa*—40 marked (18 recovered); *D. genutia*—24 (5); *E. blanda*—30 (4); *P. aristolochiae*—15 (9); *P. confucius*—32 (11); and *C. strabo*—8 (2). *Radena juventa* and *E. blanda* were marked with different colors in the Eastern Foreland and Northeast Headland, and none was recaptured in the other area. Most recaptures were within 20–40 m of the release points, with maximum distances (*R. juventa*—2, *D. genutia*—1) of about 200 m. In general, recaptures were too sporadic for reliable interpretation of population sizes but the estimates of relative abundance noted earlier incorporate inference from this study in addition to transect counts.

Leps and Spitzer (1990) compared the butterflies of forest climax, transitional, and ruderal communities in northern Vietnam by transect counts and indicated that high density and faunal heterogeneity were associated with the less advanced vegetation, whereas forest butterflies exhibited lower diversity but higher constancy. Fifty-five of the total of 82 species they recorded (Lycaenidae and HesperIIDae were excluded) had relatively broad geographical ranges, and some of these were characteristic of ruderal habitats (17 of 55 species) or forest clearings (6 of 55). If all records for each Vietnam habitat are combined, the totals for each habitat become 45 of 82 species (ruderal) and 62 of 82 (forest clearings), with a combined total of 75 species; only 7 of 82 species were confined to closed forest and all of these have restricted geographical ranges. Thus, there was a trend for broad range species to be excluded from more specialized or later succession plant associations. 'Ruderal systems' are the result of shifting agriculture, and they represent secondary simplification from the cultivation of fields derived from clearing forests and their subsequent abandonment and transformation to grasslands with low shrubs. Few such studies of habitat or successional segregation of butterflies have been made in southeast Asia, but Leps and Spitzer (1990) emphasize that many of the characteristic ruderal species are extremely good colonizers of early successional habitats, and their Vietnam list includes some of the Anak Krakatau taxa: *P. aristolochiae*, *P. memnon*, *G. sarpedon*, *C. pomona*, *E. hecabe* and *N. hylas*. In Vietnam, *T. helena* was most characteristic of forest clearings, coinciding (in part) with its habitat on Anak Krakatau.

To date, there are few true forest butterflies on any of the Krakatau islands and none on Anak Krakatau. As suitable habitat develops, some may be expected to appear—although there is a strong possibility that most such specialist species may not be sufficiently vagile to reach the islands except by rare chance. The mosaic of habitats at present available on Anak Krakatau increasingly fosters the establishment of many of

the earlier succession species that may arrive, and their persistence will depend on the continuance of the full array of such habitats, including *Ipomoea pes-caprae* communities and relatively pure grassland stands. The 'arrival wave' of butterfly species to the archipelago that is best represented on Anak Krakatau is the set that colonized the archipelago between 1908 and 1921, from 25 to 38 years after 1883, the period of forest formation. The biological age of Anak Krakatau, assuming a self-sterilizing volcanic eruption in 1952, was 38 years at the time of the last survey, and mixed forest was beginning to develop. Thornton et al. (1990) review numerous examples of the extinction of animals on the archipelago coinciding with the main period of canopy closure and elimination of more open habitats, and New et al. (1988) point out that the extinction rate for butterflies was highest during that period (1919–34). Monitoring the sequence of vegetational succession on Anak Krakatau over the next two decades could shed considerable light on the need to manage such open areas elsewhere to conserve the early successional habitats necessary for many invertebrate animals. This theme scarcely has been documented in tropical areas, especially those sufficiently distant from putative sources to render colonization by late successional 'specialist' taxa relatively difficult.

As Thomas (1991:270) commented 'Butterflies are becoming sufficiently well-studied for them to be used . . . for general conservation planning in some parts of the tropics, as a representative insect group.' His study in Costa Rica also emphasized that species frequenting modified habitats tend to be those with broad distributions, and that conservation of primary forest is necessary to conserve narrow endemic 'specialist' butterflies. Comparison with the pattern of butterfly colonization inferred on the older Krakatau islands suggests strongly that some widespread species on Anak Krakatau could be conserved locally only by maintenance of early seral stages of vegetation. For example, *D. genutia* and *P. conjunctus* appear to survive on the archipelago only because they inhabit the early successional habitats provided by Anak Krakatau. Others, such as *H. taminatus* and *P. c.f. guttatus*, may have been able to colonize the island group only because early successional habitats have been available. Altogether, some eleven butterfly species may owe their presence on the archipelago, either as recent colonists or as declining resident species, to the habitats provided by Anak Krakatau and the Sertung spit (Thornton et al. 1992). We suggest that such species will eventually disappear from Anak Krakatau as its communities move towards later successional phases. Such a move is by no means inevitable, however. Future volcanic activity could set back the succession, thus again postponing the extinction of such butterflies from the island. Rejuvenation of Anak Krakatau through sporadic vol-

canic activity may prove to be an important factor in assuring that such butterflies persist on the island.

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MASS FLIGHT RESPONSE OF OVERWINTERING MONARCH BUTTERFLIES (NYMPHALIDAE) TO CLOUD-INDUCED CHANGES IN SOLAR RADIATION INTENSITY IN MEXICO

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ABSTRACT. Seemingly enigmatic behavioral responses to sudden clouding characterize monarch butterflies in their overwintering colonies in Mexico. On sunny days throughout the overwintering season, large numbers of monarchs basking on conifer boughs within their colony repeatedly respond to periodic cloud shadow by taking flight and flying above the colony for approximately 5 minutes before reforming clusters on the boughs. Likewise, monarchs in streaming flights down an arroyo to water reverse direction and head back to their colony when shaded by a cloud. We hypothesize that both of these behaviors are physiologically triggered by rapidly lowering body temperature when solar radiation warming their bodies is obscured by a cloud. The reversal in flight direction is interpreted as an adaptation to the unpredictable duration of cloud cover which, if longer than a few minutes, would result in the butterflies' thoracic temperatures dropping below flight threshold. This could strand butterflies away from their colony for up to several days, subjecting them to freezing at night, and possibly also to greater bird predation. Within their colony, the adaptive significance of the cloud-induced behavior appears to be that it allows individual butterflies to relocate into positions on boughs that are better insulated by the forest canopy against radiant heat loss to the open sky during the night.

Additional key words: cloud-response, microclimate, thermoregulation, thermal ecology, overwintering.

Monarch butterflies, *Danaus plexippus* L., overwintering in the high mountains of the Transvolcanic Range of Mexico cannot fly until their thoracic temperatures reach 12.7–16°C (mean thermal flight threshold = 14.35°C, Masters et al. 1988). Ambient temperatures beneath the shaded forest canopy rarely exceed this flight threshold, and in one overwintering colony it was exceeded on only 2 of 46 days between 20 January and 6 March (Calvert & Brower 1986). Therefore few monarchs should be active during most of the overwintering period. However, on clear days, although the majority of butterflies remain clustered in shaded areas on the trees, hundreds of thousands sun-bask, countless others fly about above the firs in no sustained direction, while still others stream back and forth to water as far as a kilometer from the colony (Brower 1986, Calvert & Brower 1986, Masters et al. 1988). The monarchs are able to fly in the cold ambient environment because they are

extremely proficient at raising their thoracic temperatures by solar basking in either direct or diffuse sunlight: in less than a minute an individual monarch can raise its body temperature from below to well above flight threshold (Kammer 1970, Douglas 1979, 1986, Casey 1988, Masters et al. 1988).

A particularly striking behavior of these sun-basking monarchs in the overwintering colonies is that when a cloud casts a shadow, the butterflies invariably fly from their perches in such large numbers that for several minutes the sky is partially darkened (Fig. 1A,B). We first noted this reaction in January 1977 (Brower et al. 1977) and have since observed it on hundreds of occasions over 16 overwintering seasons. If the cloud shadow persists for only a short time, most butterflies land and resume basking. However, if the cloud cover persists for more than about five minutes, the monarchs flutter down and land on less exposed positions of the tree boughs within the protective cover of the forest canopy (Fig. 1B). Both the sky above the colony and the original exposed basking positions become virtually clear of butterflies. Individual butterflies sometimes follow each other in undulating chains as they reform the clusters (arrow in Fig. 1B).

Over the last 16 years, we have observed that the intensity of the cloud-response appears related both to the thickness of the cloud and to the length of sunshine preceding the cloud shadow. The most intense response occurs after a long period of cloudless sunshine and when the cloud is thick. Less intense responses occur when clouds and short periods of sunshine alternate in rapid succession and when the clouds are thin so that they only partly block the radiation falling on the colony. The cloud-response involves both an increased number of butterflies flying and an increase in the tempo of sound caused by the butterflies colliding with each other and with the vegetation. For this study, we chose a situation in which a thick cloud passed over the colony after a long period of cloudless sunshine.

We also have observed repeatedly a second cloud-induced behavior that was first reported by Brower (1986). Binocular viewing from above the colony on clear days documented huge streams of monarchs flowing out of the colony and down an arroyo in search of water. When suddenly shaded by a cloud, these streaming butterflies reverse direction back towards the colony. If the cloud passes before the butterflies reach the colony, they again switch direction towards the water sources.

In this paper we present quantitative data on the monarchs' cloud-response behavior when direct sunlight radiating the basking butterflies is obscured by a passing cloud. We then provide a common hypothesis that explains the cloud-induced flight behaviors of the butterflies both within their colonies and while flying to water sources.

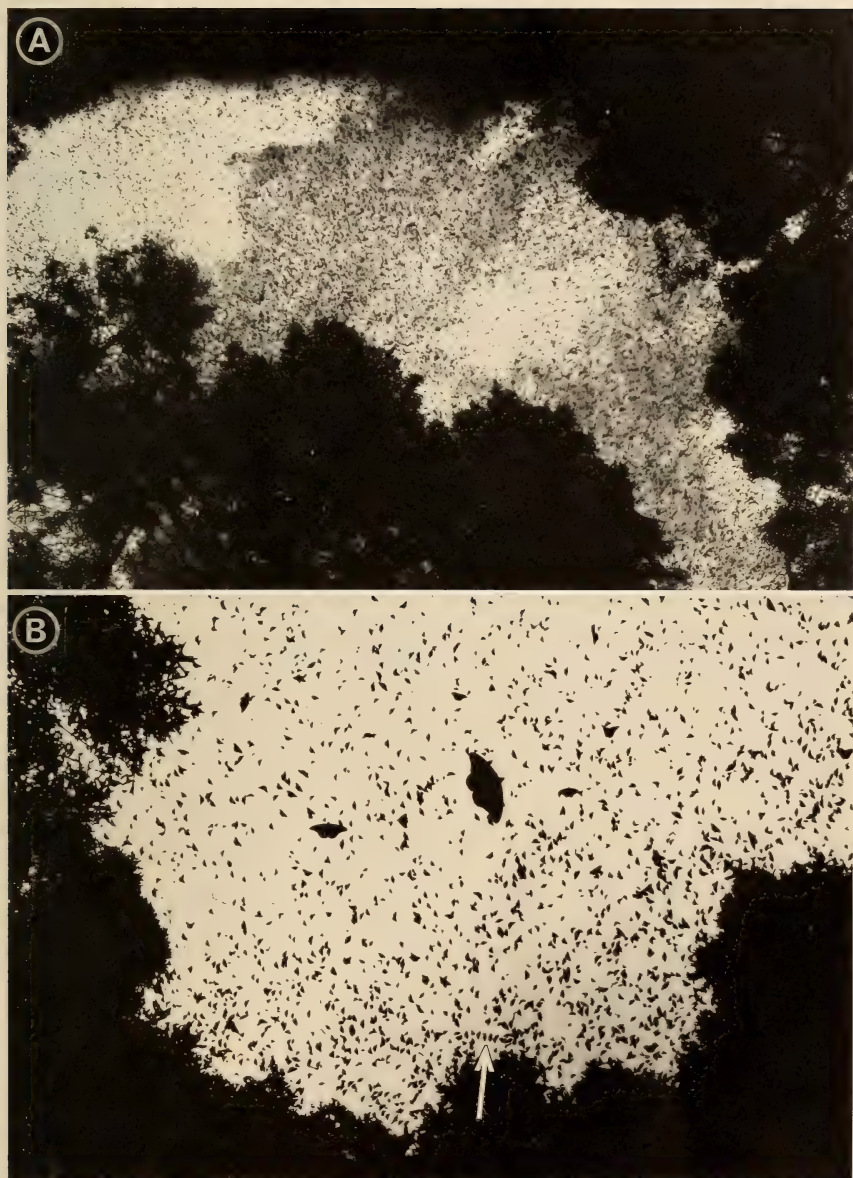


FIG. 1. Cloud-response behavior of monarch butterflies at their Sierra Chincua overwintering site in Michoacan, Mexico. A) Wide-angle view of the sky, clouds that have just shaded the area, and the *Abies religiosa* roosting trees with several thousand flying monarchs that have been stimulated by the drop in solar radiation to fly above the tree canopy (15 March 1981; original 35 mm kodachrome by L. P. Brower). B) Within about five minutes after the appearance of the cloud, the monarchs begin to reform their clusters. Individual butterflies follow each other in undulating chains (see arrow) as they fly to the tree boughs. Original 35 mm kodachrome by W. H. Calvert.

METHODS

The overwintering colony of several hundred thousand monarchs occupied 0.54 hectares of the *Abies religiosa* (Pinaceae) fir forest in the Sierra Chincua of Mexico's Transvolcanic Belt (19°41'N, 100°18'W, altitude 3000 m). The colony was on the high slopes of the Arroyo La Plancha drainage immediately below an area locally known as Peña Cargada, near the town of Angangueo, Michoacan (Calvert & Brower 1986). We estimated butterfly flight response to a cloud that rapidly obscured solar radiation on 22 January 1986, a clear to partly cloudy day. Using a Nikon 50 mm lens set at a focal distance of approximately 25 m, we took a series of 35 mm color slides of an area of sky from the same point within the colony before, during, and after the passage of a large, thick cumulus cloud. We projected 18 of these slides taken at one minute intervals from 1438–1455 h and counted the flying butterflies in each image. The field of view on the projection screen consisted of a column of air with a focal midpoint cross sectional area of approximately 20 × 30 m. While taking the photographs, we also recorded the time of appearance and duration of the shadow produced by the cloud that passed over the colony. Variation in the solar radiation was recorded simultaneously in a nearby forest clearing located ca. 0.5 km south of the butterfly photographing position. We used a pyranometer (Model No. LI-200SB) attached to a printing integrator (LI-550B; Li-Cor Inc., Box 4425, Lincoln, Nebraska 68504) to measure the incident radiation (watts per m² across the spectrum from 400 to 1200 nm) at one minute intervals from 1420–1459 h. By synchronization of the pyranometer clock and the photographer's watch, and by noting the time of onset of shading above the butterflies and above the pyranometer, we determined that it took 5 minutes for the cloud to travel from the pyranometer site to the butterfly colony. Thus Table 1 and Fig. 2 show 18 butterfly counts from 1433–1450 h with times adjusted to correspond to the pyranometer readings.

RESULTS

A few cumulus clouds appeared around the mountain massif shortly after noon on the day of our study, and high, thin cirrus clouds also were present intermittently. The radiation data and butterfly counts are in Table 1. During a cloudless period from 1420–1436 h, the average irradiance in one minute samples varied between 620–812 w/m² (mean = 745 w/m²). At 1437 h the cloud drifted between the sun and the monarch colony. During the 10 minutes that the shadow persisted (1437–1446 h), the mean radiation was 143 w/m² with a low of 102 w/m². From 1447–1459 h after the cloud passed, it varied between 501–762 w/m² (mean = 725 w/m²).

TABLE 1. Solar radiation as watts per m^2 measured at one minute intervals from 1420–1459 h and samples of the numbers of monarch butterflies flying in the sky above the canopy in the Sierra Chincua overwintering colony, 22 January 1986. Butterfly counts were made from photographs taken at one minute intervals over an 18 minute period when a cumulus cloud drifted across the forest and shaded the roosting monarchs for approximately 10 minutes.

Minutes after 14 h	Solar radiation (watts/ m^2)	No. of flying butterflies/600 m^2
20	810	—
21	812	—
22	796	—
23	798	—
24	804	—
25	801	—
26	798	—
27	798	—
28	776	—
29	745	—
30	750	—
31	716	—
32	679	—
33	637	20
34	620	16
35	662	8
36	665	9
37	249	54
38	119	193
39	113	308
40	110	232
41	105	232
42	102	263
43	102	881
44	113	766
45	142	420
46	277	419
47	501	282
48	671	194
49	668	13
50	651	56
51	702	—
52	742	—
53	728	—
54	745	—
55	753	—
56	716	—
57	736	—
58	762	—
59	626	—

Fig. 2 is a plot of the radiation data measured over one minute intervals from 1420–1459 h, and the numbers of butterflies flying at 18 one minute intervals extending from 4 minutes before to 4 minutes after the cloud passed. Flying butterflies counted in the space above

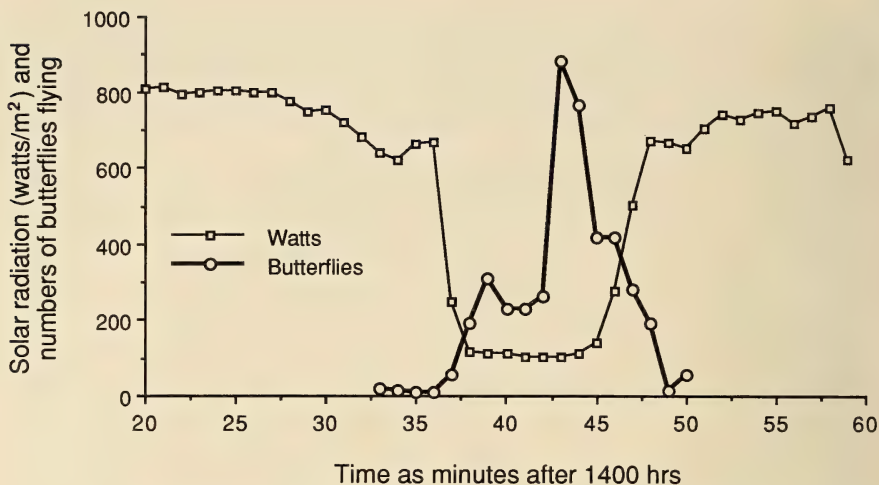


FIG. 2. Cloud-response behavior of sun basking monarch butterflies to the sudden attenuation of radiation by a cloud. Sierra Chincua, Mexico, overwintering colony, 22 January 1986. Data are from Table 1.

the camera during the last 4 minutes of the initial cloudless period (1433–1436 h) ranged from 8 to 20 individuals (mean = 13 butterflies). During the cloudy period the numbers of butterflies flying rose to 881 individuals, a 40 to 100 fold increase over the numbers flying before the cloud shadow. The cloud began passing the sun at 1444 h and the number of butterflies dwindled back to less than a hundred over the next 5 minutes.

DISCUSSION

Masters et al. (1988) experimentally determined that when sun basking monarchs were moved into the shade at an ambient temperature of 11.3°C, their thoracic temperatures dropped from 29°C to below the lower flight threshold (12.7°C) in less than 7 minutes. In the current study, we documented that the butterfly flight response within the colony is correlated with the rapidly diminishing amount of radiation caused by the passage of a cumulus cloud. Our data also indicate a 6–7 minute delay between the onset and peaking of the cloud-response (Table 1). This delay is consistent with the heat loss curve identified by Masters et al. (1988) and strongly suggests that the cloud-response is triggered by the butterflies' rapidly decreasing body temperature rather than by the decreased light intensity *per se*.

Periodic clouding occurs frequently at the Mexican overwintering sites from December through February, the coldest part of the over-

wintering season (Mosino-Aleman & Garcia 1974, Anonymous 1976, Calvert et al. 1989). Early mornings are typically clear but cumulus clouds begin to form over the mountain massifs towards noon and continue to build through the afternoon leading to partly cloudy and then often overcast late afternoons. The duration of cloud shadow is unpredictable. Thus when the first cloud appears it may cast a shadow for only a few seconds, or it may be the harbinger of complete sky closure for several days (Calvert et al. 1983).

We therefore hypothesize that taking flight and reforming clusters under the thermally insulating canopy of the forest allows individual butterflies to avoid being trapped in positions that are directly exposed to the sky. Such trapping is extremely dangerous because intense clearing at night frequently results in temperatures plummeting to as low as -5°C (Calvert & Cohen 1983, Calvert et al. 1982, 1983, 1984, 1986). This, in combination with heavy dew that forms on surfaces exposed to the open sky, greatly increases the danger of the butterflies freezing through inoculative ice crystal formation (Salt 1936, Calvert & Brower 1981, Brower 1985, Anderson & Brower 1992).

We also deduce from our research in another Sierra Chincua overwintering colony (Brower & Calvert 1985) that an additional advantage of the cloud-response behavior may be a reduction of bird predation. During the winter of 1978–79 birds consumed an average of 15,000 monarchs per day. However, the risk of predation for individual butterflies in exposed positions within the colony was greater than for individuals in clusters (see also Calvert et al. 1979, Hamilton 1971). Thus, if butterflies were to be trapped thermally while more dispersed, the probability of bird predation on individuals would be increased.

CONCLUSIONS

Two heretofore enigmatic and very different behaviors of tens of thousands of butterflies responding dramatically to cloud shadow appear to have a common proximate cause. We hypothesize that both behaviors are an innate behavioral response to the butterflies' rapid cooling that results from reduced solar radiation caused by the cloud shadow.

The ultimate evolutionary advantage of the cloud-response behavior is that it reorganizes the individual butterflies into tightly clustered positions on the boughs that are better insulated by the forest canopy against radiant heat loss to the open sky during the night. Away from the colony, the butterflies' reversal in flight direction back towards their colony prevents individuals from becoming stranded and subjected to a higher probability of freezing or being eaten while engaged in normal behaviors critical to winter survival.

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LARVAL MORTALITY OF INDIAN TASAR SILKWORM
(*ANTHERAEA MYLITTA*) (SATURNIIDAE)
DUE TO PÉBRINE INFECTION

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ABSTRACT. Large scale mortality of tasar silkworm, *Antheraea mylitta*, occurs during commercial rearing seasons because of pébrine caused by *Nosema* sp., a microsporidian pathogen. This paper reports comparative mortality by instar in pébrine free and pébrine infected larvae during three rearing seasons—rain, autumn, and winter.

Additional key words: seasonal variation, *Nosema*, pathogen, *Bombyx mori*.

Pébrine is a common disease of the tasar silkworm caused by a pathogen *Nosema* sp., which results in heavy mortality to the tasar silkworm, *Antheraea mylitta* (Drury). Little literature is available on tasar mortality due to pébrine (Jolly 1968). Most studies on pébrine have focused on *Bombyx mori* L., examining effects of temperature and humidity on pébrine occurrence (Dasgupta 1950), seasonal incidence of pébrine (Deviah & Krishnaswami 1975), and seasonal variation on larval mortality caused by pébrine (Noamani et al. 1971). Studies on drug effect and susceptibility of *Malacosoma disstria* Hübner to *Nosema distriae* have been reported by Wilson (1984) and Chandra and Sahakundu (1983). However, there is no published information on the rate of mortality of the tasar silkworm due to pébrine. Hence, this investigation was conducted during 1988 to determine the susceptibility of tasar silkworm to pébrine disease in different larval stages and different seasons.

MATERIALS AND METHODS

Mated females of *A. mylitta* were segregated into pébrine free (PF) and pébrine infected (PI) groups after microscopic examination of the moths in the grainage at the State Tasar Research Farm, Durgapur, Mayurbhanj District of Orissa, India. The grainage is a specially designed house for preservation of tasar seed cocoons and production of

healthy tasar eggs at a commercial scale. Pébrine free and pébrine infected eggs were collected after oviposition. The eggs were allowed to hatch, and twenty replications of 500 hatchlings of both pébrine free and pébrine infected *A. mylitta* were reared on *Termilalia tomentosa* Wt. & Arn. (Combretaceae) in isolated rearing fields at the State Tasar Research Farm. The mortality of pébrine free and pébrine infected larvae at each instar was tabulated. The experiment was repeated during three commercial rearing seasons, i.e., July–August (Rain), September–October (Autumn), and November–December (Winter) of 1988. The data were analyzed statistically using Student's *t*-test (Snedecor & Cochran 1967). Climatological parameters, such as maximum and minimum temperature, relative humidity, and rainfall during experimental periods were recorded.

RESULTS

Mortality of tasar silkworm is common in cultures due to outdoor rearing methods which subject them to adverse climatic conditions, predators, parasites, and diseases. Observations indicated that percentage mortality of pébrine infected larvae was greater than that of pébrine free larvae in all instars except the 5th and in all seasons. The probability values ($P < 0.001$) of the *t*-tests demonstrate a statistically significant difference in percentage mortality of pébrine free and pébrine infected larvae, except for 1st instars in the winter sample (Table 1). Mortality was consistently higher in pébrine infected larvae in instars 1–4 and in pébrine free larvae in instar 5. Within the pébrine free samples, percentage mortality was higher in the 1st and 5th instar than in the 2nd, 3rd, and 4th instar. Within the pébrine infected samples, percentage mortality was higher in the 3rd and 4th instar than in the 1st, 2nd and 5th instar.

DISCUSSION

Sen et al. (1969) reported that mortality of *A. mylitta* larvae was accelerated from the 3rd instar onwards, with increasing intensity of disease symptoms. However, the present investigation indicated that the pathogen was most active and virulent during the 3rd and 4th instars inducing maximum mortality. This is similar to earlier observations by Wilson (1984) in *M. distriæ* in which he concluded that 3rd instar larvae are more susceptible than 5th instar larvae.

Comparatively lower percentage mortality in pébrine infected larvae in the 5th instar may be due to elimination of larvae susceptible to the pathogen in the 3rd and 4th instars, a possible inactive phase of the pathogen in the 5th instar, or the development of immunity in the surviving larvae.

TABLE 1. Percentage mortality \pm standard deviation of pébrine free (PF) and pébrine infected (PI) larvae of *A. mylitta* at different instars and during different seasons of 1988.

Season	Larval condition	1st instar	2nd instar	3rd instar	4th instar	5th instar
Rain	PF	18.11 \pm 1.23	12.94 \pm 1.38	11.84 \pm 1.20	10.90 \pm 1.21	15.50 \pm 1.29
	PI	19.13 \pm 1.57	13.55 \pm 1.60	22.90 \pm 1.68	28.54 \pm 1.35	8.27 \pm 1.55
	<i>t</i> =	<i>P</i> < 0.001	<i>P</i> < 0.001	<i>P</i> < 0.001	<i>P</i> < 0.001	<i>P</i> < 0.001
Autumn	PF	20.17 \pm 1.24	13.25 \pm 1.28	12.11 \pm 1.18	11.80 \pm 1.57	16.53 \pm 1.18
	PI	21.40 \pm 1.31	14.43 \pm 1.57	24.06 \pm 1.23	30.34 \pm 1.56	9.15 \pm 1.55
	<i>t</i> =	<i>P</i> < 0.001	<i>P</i> < 0.001	<i>P</i> < 0.001	<i>P</i> < 0.001	<i>P</i> < 0.001
Winter	PF	15.96 \pm 1.91	10.48 \pm 1.20	8.19 \pm 1.36	8.59 \pm 1.18	13.22 \pm 1.26
	PI	16.04 \pm 1.96	11.41 \pm 1.57	19.54 \pm 1.19	25.09 \pm 1.31	6.45 \pm 1.38
	<i>t</i> =	NS*	<i>P</i> < 0.001	<i>P</i> < 0.001	<i>P</i> < 0.001	<i>P</i> < 0.001

* NS = Not significant.

TABLE 2. Mean values \pm standard deviation of some environmental parameters during different rearing seasons of *A. mylitta* during 1988.

Parameters	Rain	Autumn	Winter
Daily maximum temperature ($^{\circ}\text{C}$)	35.17 ± 1.68	34.40 ± 1.39	29.70 ± 1.28
Daily minimum temperature ($^{\circ}\text{C}$)	22.78 ± 1.23	20.33 ± 1.18	16.27 ± 1.14
Daily relative humidity (%)	91.40 ± 1.78	90.00 ± 1.89	81.67 ± 1.58
Total rainfall (mm)	312.50	142.83	20.83

The average temperature, relative humidity, and rainfall were all least during winter, coinciding with the lowest larval mortality. These climatic features were highest during 'rain' and medium during 'autumn' (Table 2). The medium temperature and relative humidity regimes coincide with highest larval mortality, which is similar to observations by Dasgupta (1950) in *B. mori*. Medium temperature and relative humidity apparently stimulate the pathogen. However, Deviah and Krishnaswami (1975) found minimum incidence of pébrine in *B. mori* at higher temperature and relative humidity, and maximum incidence at low temperature and relative humidity. In contrast, Noamani et al. (1971) reported that temperature and relative humidity have no relation to incidence of pébrine. Although our data and results are consistent with the findings of some previous studies regarding the role of climatic factors on the mortality of pébrine infected *A. mylitta*, they are contrary to those reported in other studies. Hence, it is clear that this topic requires further investigation.

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SEXUAL DIFFERENCES IN HABITAT PREFERENCE
AND BEHAVIOR OF *OENEIS CHRYXUS*
(NYMPHALIDAE: SATYRINAE)

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ABSTRACT. Individual *Oeneis chryxus* were captured, marked, released, and observed during 1988 and 1990 at a site in the Rocky Mountains of central Colorado at 2700 m. Habitat preferences were analyzed in the context of hilltopping and territoriality. Males showed a clear preference for rocky ridge tops, whereas most females were found in grassy meadows. Male and female flight patterns differed significantly. Males and females responded differently to conspecifics and to other species. Males defended territories, females did not.

Additional key words: hilltopping, territoriality, flight pattern, mate-searching, arctic butterfly.

Oeneis chryxus (Doubleday and Hewitson) is a small, orange-brown, cryptically-colored butterfly. It prefers open, sunny habitats, and is arguably the most variable of the "arctics" in terms of color, markings, habitat, range, and behavior. This species is found in northern or montane environments characterized by short summers and requires two years to mature. At least one population in Colorado is synchronized on a biennial cycle, with adults absent in odd numbered years (Emmel et al. 1992, Clayton & Petr, unpublished). Scott (1986) reported that population size is greater during even-numbered years in Colorado and in odd-numbered years in northwest Wyoming and California; alternating population size is not apparent in Michigan and Manitoba (Scott 1986).

Masters and Sorensen (1969) characterize *O. chryxus* as a prairie and steppe species with a tendency to move into other habitats such as forests and mountaintops. At Stagecoach Meadows, on the west slope of the Colorado Rockies (Gunnison County, Colorado), *O. c. chryxus* occurs in open meadows but is found more often in the "tension zone" between meadow and forest, characterized by fallen trees and open areas for perching (Masters & Sorensen 1969). Scott (1986) reported *O. c. chryxus* perching on hilltops or ridge tops, but also observed the species perching in gulches near timberline in the San Juan Mts., Colorado (perhaps to avoid harsh winds that sweep the crests). Other species of *Oeneis* (e.g., *O. melissa* (Fabricius)) also are known for their hilltopping habits (Troubridge et al. 1982). Dunlap (1962) and Knapton (1985) studied *O. c. strigulosa* McDunnough in Algonquin Park, Ontario, Canada, where it reportedly does not exhibit hilltopping behavior but defends perch sites in open sandy or stony spots in relatively flat terrain. In addition, territorial behavior has been reported for *O. chryxus* by Dunlap (1962), Troubridge et al. (1982), Knapton (1985), and Mas-

ters and Sorensen (1969), and for several other species of *Oeneis* by Guppy (1962), Masters and Sorensen (1969), and Troubridge et al. (1982).

Based on studies of *O. c. chryxus* in a montane community near Florissant, Colorado, we report on sexual differences in habitat preference, territoriality, and behavior.

MATERIALS AND METHODS

Our study area was located 12 km S of Florissant, Colorado, at an elevation of 2670–2707 m. It was traversed by a path 1065 m long, connecting three ridge tops (A, B, & C) and two meadows (MB & MC). The study area covered 102,850 m² of which ridges were 10,450 m² and meadows were 18,400 m².

The ridges were characterized by rock outcroppings, pines (*Pinus ponderosa* Laws.; Pinaceae), aspens (*Populus tremuloides* Michx.; Salicaceae), and open patches of stony soil sparsely vegetated with low grasses and forbs. Meadows were located at the base of large gulches where soil was deeper, richer, and wetter. Meadows supported grasses and forbs with shrubby cinquefoil (*Potentilla fruticosa* L.; Rosaceae) and other shrubs sparsely distributed throughout, and small aspens and pines around the edges.

Observations were made on 4 days (5–8 July) in 1988 and on 13 days (24 June–6 July) in 1990. A total of 196 individuals were captured, marked, and released. Individual *O. c. chryxus* were numbered on the underside of the hindwing using red or black Sharpie permanent marker pens (Sanford) or a "Silver-Marker" paint-pen (Pilot) and identified later with binoculars. Each individual's number, sex, location of capture, and the time, date, and location of all sightings and behaviors were recorded. Some individuals were sighted 10 or more times per day but were counted only once per day unless they moved to a different ridge or meadow. This procedure prevented biases from extended observations at more active sites.

RESULTS

Habitat Preference

Ridge tops and meadows. Males were found more frequently on ridge tops, and females were found more frequently in meadows (Fig. 1; Chi Square with Yates correction = 157.5, $P < 0.001$). The pattern of sex distribution on the ridges was the same in 1988 and 1990.

Females were more sedentary than males. Fifteen percent (26 of 173) of adults captured in 1990 were females, but only 10.5% of the sightings (29 of 275) were females.

Elevation and exposure. Fig. 2 gives the number of male sightings

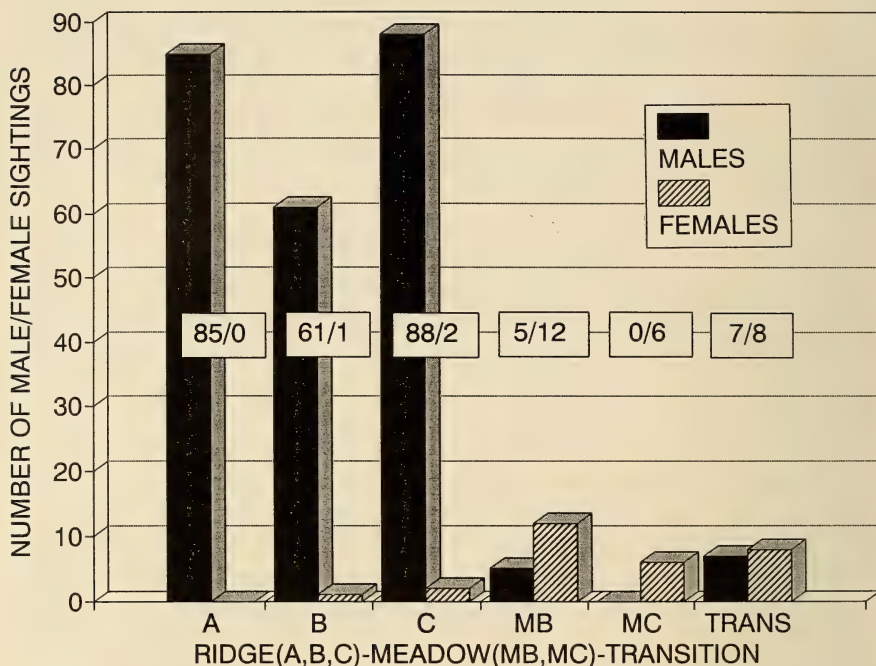
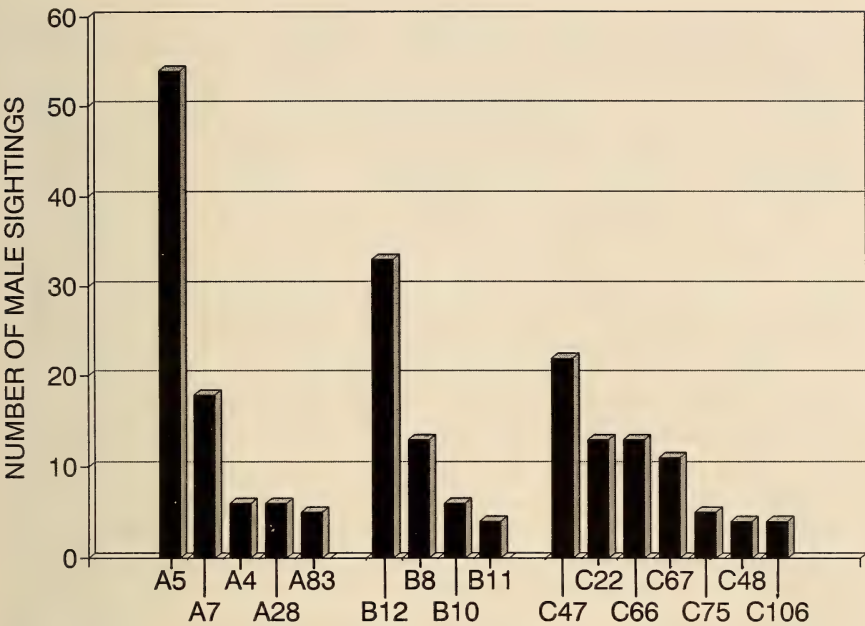


FIG. 1. Habitat distribution of male and female *Oeneis chryxus chryxus* sightings at three ridge tops, two meadows and intermediate areas (TRANS). Numbers in boxes indicate the proportion of males to females for the 1990 season. Individuals were scored only once per day.

at the more active perch sites during the 1990 season. Elevation of perch sites and number of male sightings showed a significant positive correlation (Spearman Rank Correlation, $P < 0.05$). Perch sites A5, B12, and C47 were the three most frequently occupied and also were the highest sites on the three ridges of the study area. Ridge C was not studied in 1988, but activity on Ridges A and B showed the same pattern in 1988 as in 1990, with sites A5 and B12 being the two most active sites, and A7 and B8 being next most active. All active sites (Fig. 2) were open and relatively free of ground cover and overhead vegetation.

Behavioral Differences

Flight patterns. Females seem to have a slower wing-beat, fly with less undulation, and have straighter flight paths than males. By contrast, males circled and returned quickly to their perches after engaging other butterflies or if disturbed by us. These simple differences were used to correctly predict sex of 60/60 male and 11/12 female *O. c. chryxus* before capture ($P < 0.001$, Chi Square = 45.9). When stalked or disturbed, males sometimes abandoned the perch and disappeared into



THE MOST ACTIVE RIDGE SITES

FIG. 2. Number of *Oeneis chryxus chryxus* male sightings at the most frequented sites on three ridges. Sites A5, B12, and C47 were the highest points on Ridges A, B, and C. Only sites with four or more sightings are shown. Individuals were scored only once per day.

vegetation; female wing beat frequency increased or became more erratic as they attempted escape. Prediction of sex was not attempted if an individual gave conflicting signals. Predictions were recorded only during the last nine days of the 1990 field observations.

Chases and spirals. Any butterfly moving near a male *O. c. chryxus* elicited a chase. Usually the intruder took a direct path away from the perch site with the resident in pursuit. The chase often turned into a spiraling flight with two, or occasionally three, individuals twirling in tight circles around each other. Some spirals lasted more than 45 seconds and did not end until the butterflies were well above the treetops, as high as 30 m above ground. Spirals ended with one or both participants diving sharply toward the ground. The resident returned to the perch site more often than the intruder (Table 1, Chi Square = 98.7, $P < 0.001$). A resident was defined as a marked *O. c. chryxus* male with a recent history of occupancy and successful defense of the perch site against conspecifics.

Nine females captured in meadows were released on ridges and

TABLE 1. A comparison of site tenacity for resident *Oeneis chryxus chryxus* and intruding conspecifics. A resident was defined as a marked *O. c. chryxus* male with a recent history of occupancy and successful defense of the perch site.

Flight season	Return to perch site			Number of encounters
	Resident only	Intruder only	Resident and intruder	
1988	40 (88.8%)	1 (2.2%)	4 (8.8%)	45
1990	114 (77.0%)	3 (2.0%)	31 (20.9%)	148

observed. Most females fled resident males and were pursued in long chases or spiral flights. Three of the nine pursued females landed on the trunks of trees or in branches as high as 10–12 m, and the resident males returned to their perches. Only one male from more than 300 male/male encounters landed in a tree. Two of the released females landed on the ground where the pursuing males approached and attempted to mate.

Females were never observed to initiate chases or defend territories. One female was observed for an hour while nectaring on shrubby cinquefoil in a meadow. A grasshopper and six butterflies (a skipper, two angle-wings, a sulfur, a little blue, and a copper) flew within 10–30 cm of her but elicited no response. All males we observed gave chase when approached by butterflies, moths, birds, falling leaves, and even pebbles tossed near the perch.

DISCUSSION

Marked butterflies could be identified with binoculars, making it unnecessary to recapture them or to disrupt their activities. Morton (1984) found that adding marks of different color or size to the cryptic underwings of five butterfly species did not change the statistical probability of sighting them on subsequent days. Recapture involving handling, however, did reduce the frequency of sightings in his study.

Dunlap (1962) and Knapton (1985) studied *O. c. strigulosa* in Algonquin Park, Ontario, Canada, where it reportedly does not show hilltopping behavior. Both Dunlap's and Knapton's observations were made along an abandoned railroad right-of-way, raised slightly above the surrounding area and providing perch sites free of vegetation. Baughman and Murphy (1988) show that hills need not be high to orient a butterfly's movements and to evoke hilltopping. It could be argued that the Ontario population of *O. c. strigulosa* was hilltopping on the raised roadbed, but it would be difficult to make that argument for the Stage coach Meadow population of *O. c. chryxus* on the west slope of the Colorado Rockies, because they defend perches considerably below available peaks (Masters & Sorensen 1969). Whether the behavioral

variability between populations reflects genetic differences or is in response to differences in habitat, elevation, or topography is unknown.

Oeneis c. chryxus hilltop near Florissant, Colorado, although features other than elevation, such as bare ground and lack of surrounding trees or bushes, add to the attractiveness of perch sites. On ridge A, site A7 was at the same elevation as A5 and only 50 m away, but had significantly fewer male sightings (Fig. 2; Chi Square = 18.0, $P < 0.001$). The more active site (A5) had slightly less cover on the periphery and was at the head of a valley leading from a meadow. Site B8, on ridge B, was slightly lower but had more activity than adjacent sites B10 and B11. B8 was free of vegetation and atop a large rock (2 m high and 5 m in diameter), with bare ground sloping downhill for 20–25 m. B10 and B11 were bounded by bushes and trees. The distribution of *O. c. chryxus* males at sites on Ridge C are strongly correlated with elevation. Site C47 was at the peak; sites C22, C66, and C67 were at nearly equal elevations but lower than C47, and the remaining sites were even lower on the ridge.

A female would encounter a male about 15–30 times as frequently on ridges as she would in meadows. This estimate is based on male sightings and is corrected for observation times in the two habitats. Weather conditions permitted an average flight period slightly longer than five hours per day; thus, in 10 to 20 minutes a female would encounter as many males on ridges as she would in five hours (an entire day's flight period) in meadows. Hilltopping for mate location greatly reduces a female's energy expenditure and exposure to predation.

Hilltopping is well-documented for butterfly species and other insects as an efficient strategy for bringing mates together (Alcock 1987, Shields 1967, Lederhouse 1982, Scott 1968, Thornhill & Alcock 1983, Wickman 1987, 1988). We assume that virgin female *O. c. chryxus* hilltop for mating, but quickly return to meadows for oviposition on the abundant grasses that are their larval food plants. Wickman (1988) showed that virgin female *Lasiommata megera* (L.) (Satyrinae) fly uphill to where males perch, but cease to do so after mating.

Wickman (1986, 1987, 1988) and Wickman and Wiklund (1983) demonstrated that females of three genera of satyrines in Europe mate soon after eclosing and usually only once. Wiklund (1982) also showed that following mating, female *Aphantopus hyperanthus* (L.) (Satyrinae) become more cryptic, evasive, and resistive to male contact. Similar behaviors in *O. c. chryxus* likely account for the smaller number of females found in our study and in collections we have examined.

Male *Coenonympha pamphilus* (L.) (Satyrinae) defending territories achieve more matings than do males without territories (Wickman 1985). Ehrlich and Wheye (1986, 1988) present an interesting exception

in which hilltopping and territoriality result in lower mating success for *Euphydryas editha* (Boisduval) (Nymphalinae) during years of high population density (also see Scott 1968).

Territoriality in insects, and specifically in butterflies, has been questioned on the basis of the primitive phylogenetic position of the group and a lack of defensive accouterments (Scott 1974, 1986, Suzuki 1976). However, an individual's ability to maintain a territory can be decided simply by the response of conspecifics. The chases and spirals initiated by resident males are effective because intruders tend to leave directly and quickly (Table 1). The most active sites were at times contested for by two, rarely three, sparring males; but the resident initiated most of the chases, occupied the preferred perch, and enjoyed the most occupancy time. Such contests always were resolved, usually with one encounter. Encounters from which both resident and intruder returned to the perch site involved a short series of engagements from which the resident (usually) returned alone the final time. Extended observations at the more active sites in 1990 account for the increased proportion of encounters where both resident and intruder returned (Table 1).

It is unlikely that *O. c. chryxus* males can distinguish gender or even species from the perch, demonstrated by the fact that they chase skipper, swallowtails, birds, falling leaves, or tossed pebbles. Scott (1986) calls chases and spirals "potential courtship forays." The simplest explanation for these forays probably involves a fixed-action pattern (pursuit), coupled to a sign stimulus (movement) via an innate releasing mechanism (Colgan 1989). Once initiated, the behavioral sequence exhibited by the resident is switched to "sparring" by intruder males, "courtship" by females, and "break off" by other species and inanimate objects. The quickness with which resident males attempted to mate females landing on the ground suggests that males discriminate the sex of conspecifics in flight. Occasionally, sparring males landed near one another but two males were never observed to make physical contact on the ground.

The perching male does discriminate some features of intruders. He seldom chases dipterans or hymenopterans even though some are as large as some butterfly species that are chased. The most obvious difference is wing beat frequency. *Oeneis c. chryxus*, other butterflies, moths, and skippers have fluttering, undulating flight patterns and are chased. Bees and flies at most elicited brief, quickly aborted chases, as did pebbles tossed above perching males.

It is axiomatic that benefit must exceed the cost of a behavior (Carpenter 1976). The resource(s) contested for at these perch sites has not been identified unquestionably, but the most likely resource is "mates."

Ridges provide no apparent advantage for food, shelter, thermoregulation, oviposition sites, or freedom from predators.

The habitat and behavioral differences we have described for *O. c. chryxus* indicate a reduced time and energy expenditure for females. Males are found at predictable, easily-located sites (ridges); females are found away from males in more protected sites (meadows) where they are less likely to be disturbed while ovipositing. Males spend much energy and risk greater exposure defending perch sites against competing conspecific males, which suggests that natural selection pays males well for territorial defense (Riechert 1988).

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BUTTERFLIES OF THE CAYMAN ISLANDS, WITH THE DESCRIPTION OF A NEW SUBSPECIES

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ABSTRACT. Thirty-one butterfly species are recorded from the islands of Grand Cayman and Cayman Brac, including two new records for the Cayman Islands, *Eumaeus atala* and *Eurema dina dina*. *Dryas iulia zoe*, new subspecies, is described, and some aspects of the taxonomy of Cayman Lepidoptera are discussed.

Additional key words: Caribbean biogeography, *Dryas iulia zoe* n. ssp., new records.

The junior author, in the company of Z. M. Schwendeman, collected on Grand Cayman and Cayman Brac islands between 31 October and 7 November 1990. During this time, they captured a total of 407 specimens representing 31 butterfly species, one with a different subspecies on each island, and one represented by a new subspecies described herein. Two new records for the Cayman Islands are included in this total. The presence of new records on the Caymans is rather surprising; one has been led to believe that these islands are well collected. The records enumerated below raise the total number of butterflies known from these islands to 46 species, and the Grand Cayman total number of species remains at 41 species (Schwartz et al. 1987: 147), while the total for Cayman Brac is now 30 species.

Five separate localities were collected on Grand Cayman, whereas six were visited on Cayman Brac. These are discussed briefly below, and will be referred to only by code number in the text. Unless otherwise indicated, all specimens are deposited in the Allyn Museum collection, but may be distributed later.

Station GC-1 was 1.3 km N of Frank Sound, Grand Cayman, visited on 31 October. The locality was one of secondary scrub.

GC-2 was the South Sound shore area, Grand Cayman, visited on 31 October and 2 and 4 November in an area of beach scrub.

GC-3 is the Great Beach, north of a quarry, Grand Cayman, collected on 31 October and 2 and 3 November. This locality had tall scrub, apparently undisturbed.

GC-4 is Seven Mile Beach, Grand Pavilion Hotel, Grand Cayman, collected on 1, 2, and 3 November in primarily grass and weeds adjacent to the parking area.

GC-5 is Prospect Park, off Mahogany Way, Grand Cayman, collected only on 2 November. Collecting was done along dike roads near Milords Bay.

CB-1 is the Brac Reef Resort, Cayman Brac, collected only on 4 November.

CB-2 is the South Side road between Jennifer and Pollard Bays, Cayman Brac, collected on 4, 5, and 7 November, secondary scrub and trees below cliff.

CB-3 is along Stake Bay Bluff Road and Major Donald Road, Cayman Brac, visited daily from 4–7 November. This area was wooded and grassy land with many cycads.

CB-4 is Spot Bay, Cayman Brac, collected on 5 November, secondary scrub.

CB-5 is the Ashton Rutty Centre, Cayman Brac, at light, collected only for moths.

CB-6 was at Hawksbill Bay along the South Side road, Cayman Brac, collected on 6 and 7 November. This locality had secondary tree growth, was below the cliff and was shielded from the prevailing winds; it falls within the area encompassed by CB-2.

All specimens are labeled with "Allyn Museum / Acc. 1990-18", and these data will not be repeated further.

BUTTERFLIES RECORDED

Danaidae

Danaus plexippus plexippus (Linnaeus, 1758): A single female was collected at GC-2 on 31.x.1990. This record is remarkable because Askew (1980: 878) mentions that this species had not been seen on Grand Cayman since 1975, and Schwartz et al. (1987) do not mention records of it at all. The latter authors consider Cayman material to belong to the subspecies *megalippe* (Huebner, 1826), but the female at hand is clearly the migratory North American morph.

Danaus gilippus berenice (Cramer, 1779): A single male, GC-3, 31.x.1990.

Nymphalidae

Agraulis vanillae insularis (Maynard, 1889): Many specimens captured at stations GC-2, GC-3, GC-4, GC-5, CB-1, CB-2 and CB-6 (including a pair *in cop.*, 6.xi.1990).

Dryas iulia zoe Miller and Steinhauser, new subspecies

(Figs. 1–4)

This butterfly is apparently the morph that has been considered to be identical with the Bahamian subspecies, *D. i. carteri* (Riley, 1926). It previously was unreported from Cayman Brac, and a solitary male from Grand Cayman (May, M. Simon) does not appear to agree with the material at hand, but it was collected earlier in the year, and such variation must be seasonal.

Diagnosis: Male: upper surface ground color rich golden orange with a prominent black forewing cell-end bar (occasionally with a subsidiary blackening of the basal part of M_3) and very narrow black margins of both wings (hindwing margin even narrower



FIGS. 1-4. *Dryas iulia zoe* Miller and Steinhauser, new subspecies: **1, 2**, holotype ♂, upper (1) and under (2) surfaces: GRAND CAYMAN I[SLAND]: Great Beach area N of quarry; Sta. GC-3; 31.x.1990 (S. R. Steinhauser & Z. M. Schwendeman); Allyn Museum photographs 911105-15/16; **3, 4**, paratype ♀, upper (3) and under (4) surfaces: CAYMAN BRAC I[SLAND]: Hawksbill Bay, south side of road; Sta. CB-6; 6.xi.1990 (S. R. Steinhauser & Z. M. Schwendeman); Allyn Museum photographs 911105-19/20. Scale line = 20 mm.

than in *carteri*). Under surface ground color reddish tan (not as purplish as in *carteri* and not as orange as in *delila* (Fabricius 1775)); dark brown fore- and hindwing markings more clearly developed than in *carteri* and about comparable with those of *delila*; white hindwing subcostal, apical and tornal markings comparable to those of *carteri*. Length of forewing of holotype male 42.5 mm, those of the nine male paratypes range from 33 to 44 mm, averaging 40.3 mm. Female: upper surface ground color browner than in other subspecies with darker forewing shading in base of cell and distad on the wing along Cu_2-2A ; a broad fuscous band across end of forewing cell and distad along M_3 to outer margin (this band always interrupted in *carteri*); submarginal dark forewing band scalloped basad on M_3 and M_2 ; hindwing marginal band enclosing submarginal tan spots. Under surface ground color dull grayish tan and dull brown markings as illustrated and similar to those of *nudeola* (Bates, 1934) (Alayo & Hernandez 1987: pl. 18). Lengths of the forewings of three female paratypes are 39.5, 39.5 and 38.0 mm.

Male and female genitalia as in other *D. iulia* populations.

Variation: Assuming the Simon specimen gives an accurate impression, the upper side coloration and maculation are similar to the autumn specimens at hand. The under side is much more uniform and slightly redder than described.

Described from 13 specimens, ten males and three females, from the Cayman Islands.

Holotype male: GRAND CAYMAN I[SLAND]: Great Beach area N of quarry; Sta. GC-3; 31.x.1990 (S. R. Steinhauser & Z. M. Schwendeman).

Paratypes: Same data as holotype, 1 male, 1 female; same data as holotype, but 2.x.1990, five males; "Grand Cayman", 27.v.1979 (M. J. Simon, Acc. 1979-16), one male; CAYMAN BRAC I.: Hawksbill Bay, South Side rd.; Sta. CB-6; 6.xi.1990 (S. R. Steinhauser & Z. M. Schwendeman); two males and two females (including one pair *in cop.*).

Disposition of type-series: Holotype male, eight male and three female paratypes in Allyn Museum of Entomology; one male paratype in collection of M. J. Simon.

Discussion: It has always seemed odd that the Caymans should harbor a population of the Bahamian *D. i. carteri*, as claimed by Riley (1975:

87). Other isolates of *iulia* have achieved a remarkable radiation of subspecies in the West Indian islands, so the presence of a Cayman endemic is neither startling nor surprising. The present insect is perhaps nearer the Cuban *nudeola*.

Seasonal variation in *Dryas*: All of the subspecies of *D. iulia* from the northern West Indies and south Florida are very similar, displaying limited seasonal variation, most prominent on the under surface. Without exception, specimens collected during the dry season (roughly December to May) show very little patterning ventrally, whereas specimens from the corresponding wet season are strongly patterned. Certainly this explains the variation shown in the series of *D. i. zoe*, where the available dry season specimen is almost entirely devoid of patterning, especially on the under hindwing, that distinguishes the illustrated holotype and the remaining specimens in the type series. Females have the costa of the upper hindwing concolorous with the rest of the wing and are typical of the "Antillean group" of subspecies (Clench 1975) and contrasting with that of the Jamaican *D. i. delila*.

This variation is equally prominent in all populations of *D. iulia* from an area delimited by Florida, the Bahamas, and Jamaica, whereas specimens from further east and south in the Antilles do not illustrate this variation so dramatically.

To differentiate the present subspecies, other northern Antillean *iulia* are compared in Table 1.

Etymology: This insect is named after Zoe M. Schwendeman who sponsored the Cayman expedition and collected much of the type series while accompanying the junior author.

Heliconius charitonia ramsdeni W. P. Comstock and F. M. Brown, 1950: Five males were taken at stations CB-2, 5.xi.1990, and CB-6, 6.xi.1990. Comparison of Cayman material with that from Cuba and Jamaica reveal that the Cayman butterflies are referable to *ramsdeni*. This butterfly is well-known from all of the Caymans. The Allyn Museum has a pair from Grand Cayman (May, 1979, M. J. Simon). The Cayman population of *charitonia* flew higher and more rapidly than did others that we have observed in Florida, Latin America, or elsewhere in the Caribbean.

Euptoieta hegesia hegesia (Cramer, 1779): Very common on both islands. Nineteen specimens were collected at GC-2 (31.x and 2.xi.1990), GC-3 (2.xi.1990), CB-2 (5.xi and 7.xi.1990), and CB-6 (6.xi.1990).

Phycodes phaon (W. H. Edwards, 1864): Abundant only on Grand Cayman, where it previously was recorded. Twenty-five specimens were collected at GC-2, GC-3, GC-4, and GC-5 between 31.x.1990 and 3.xi.1990.

Junonia evarete zonalis (C. and R. Felder, 1865): This insect was encountered only on Grand Cayman with records from GC-2, GC-3, GC-4, and GC-5, 31.x.1990–3.xi.1990. It was sympatric with the next species at GC-3, 2.xi.

Junonia genoveva (Cramer, 1779): This butterfly was somewhat commoner than the last; 14 specimens were collected at stations GC-1, GC-3, CB-2, and CB-3 on most dates. We suspect that Schwartz et al. (1987) have confused this species with the last: whereas we record *J. evarete* only from Grand Cayman, those authors record only *J. genoveva*, and the records for Little Cayman and Cayman Brac are similarly reversed. We follow Turner and Parnell (1985) in our treatment of *Junonia*.

TABLE 1. Comparative attributes of selected populations of *Dryas iulia* from Florida and the West Indies (*D. i. delila* from Jamaica excluded as discussed in the text).

Character	Taxon			
	<i>largo</i>	<i>carteri</i>	<i>nudeola</i>	<i>zoe</i>
FW cell spot		rectangular	broadest costad	rectangular
FW streak in M ₃ -Cu ₁	always present	always present	present >90%	present 10%
FW margin	proximal teeth M ₂ -M ₃ , M ₃ -Cu ₁	proximal teeth M ₂ -M ₃ , M ₃ -Cu ₁	proximal teeth M ₂ -M ₃ , M ₃ -Cu ₁	smooth, no teeth
underside ground color	sandy shaded orange	sandy with a purple wash	sandy shaded orange	sandy shaded orange
underside ground color	tan, lightly marked with brown	tan, heavily marked with brown	tan, lightly marked with brown	tan, heavily marked with gray-brown

Anartia jatrophae jamaicensis (Moeschler, 1886): This species is another not known from Cayman Brac, and specimens were collected only on Grand Cayman at GC-2, GC-3, GC-4, and GC-5 between 31.x.1990 and 3.xi.1990.

Memphis echemus danielana (Witt, 1981): Two tattered females of this insect were collected on Cayman Brac (CB-6, 6.xi.1990). The insect is well known from there; and the Museum also has specimens from Grand Cayman.

Lycaenidae

Eumaeus atala (Poey, 1832): The discovery of a large and thriving colony of this most unexpected butterfly on Cayman Brac was perhaps the high point of the trip. A total of 58 specimens were collected, 53 at CB-3 during the period from 4-7.xi.1990, and five at CB-6 on 6-7.xi.1990; others were observed, but not captured at CB-1. They represent a new record not only for Cayman Brac, but also for the Caymans as a whole. There were abundant cycads in the area of karst topography at CB-6.

Strymon martialis (Herrich-Schaeffer, 1864): Two specimens of this insect were taken at GC-4 on 1-2.xi.1990. It also is known from Little Cayman, but not yet from Cayman Brac.

Strymon acis gossei (W. P. Comstock and Huntington, 1943): Two specimens were collected at GC-2 (2.xi.1990) and CB-6 (7.xi.1990). Both are referable to the Jamaican subspecies despite assignment of Cayman Brac material to the Cuban *S. a. casasi* (Comstock and Huntington, 1943) by Schwartz et al. (1987: 147).

Leptotes cassius theonius (Lucas, 1857): This butterfly was encountered on both islands, whence it has been reported previously. Specific records are GC-4 (3.xi.1990), CB-1 (4.xi.1990), CB-2 (5.xi.1990), and CB-6 (7.xi.1990).

Hemiargus hanno filenus (Poey, 1832): Known from all of the Caymans, specimens were taken at GC-1 (31.x.1990), GC-3 (2.xi.1990), GC-4 (2 and 3.xi.1990), CB-2 (5.xi.1990), and CB-6 (6.xi.1990).

Cyclargus ammon erembi Nabokov, 1948: This striking Cayman endemic is known from all three islands, and 49 examples were collected on GC-2, GC-4, CB-1, CB-2, and CB-4 between 31.x and 5.xi.1990. One pair was taken *in cop.*, GC-4, 2.xi.1990.

Pieridae

Appias drusilla poeyi (Butler, 1872): Well known from the Caymans, a few specimens were collected at CB-2 (4 and 5.xi.1990) and CB-6 (6-7.xi.1990).

Ascia monuste eubotea (Godart, 1819): Another butterfly of wide occurrence, this species was taken at GC-3 (31.x and 2-3.xi.1990), GC-4 (3.xi.1990), CB-2 (4-5.xi.1990), and CB-6 (6-7.xi.1990).

Phoebis sennae sennae (Linnaeus, 1758): Recorded from all three Cayman Islands, single specimens were taken at GC-3 (2.xi.1990) and CB-6 (6.xi.1990).

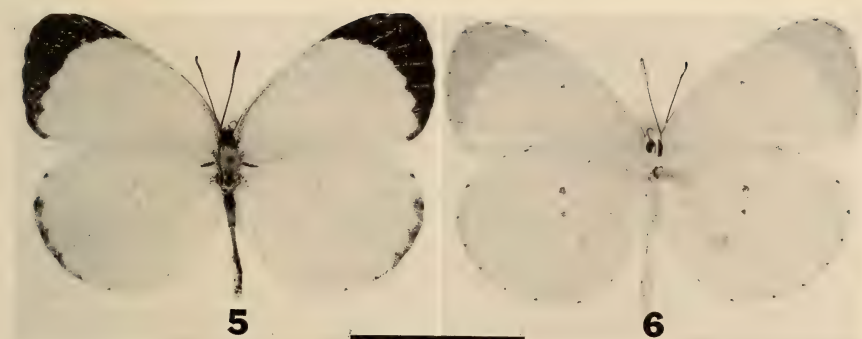
Eurema daira palmira (Poey, 1852): This widespread species was encountered at GC-3 (31.x and 2.xi.1990), GC-4 (2.xi.1990), CB-1 (4.xi.1990), CB-2 (4.xi.1990), and CB-6 (7.xi.1990).

Eurema elathea (Cramer, 1775): This butterfly exhibited a more restricted range than the last and was collected at GC-3 (31.x and 2.xi.1990) and CB-1 (4.xi.1990). The latter record is the first from Cayman Brac (Schwartz et al. 1987: 147).

Eurema nicippe (Cramer, 1782): Recorded from all of the Caymans, a single specimen was taken at GC-3, 2.xi.1990.

Eurema lisa euterpe (Menetries, 1832): This widespread species was encountered only on Grand Cayman, though it is known from all of the Caymans (Schwartz et al. 1987: 147). Specimens were taken at GC-1 (31.x.1990), GC-2 (2.xi.1990), and GC-3 (31.x.1990).

Eurema nise nise (Cramer, 1775): This butterfly, described from Jamaica (Riley 1975: 120) and recorded from Cuba (Alayo & Hernandez 1987: 76-77), is newly recorded from the Cayman Islands on the basis of a single male taken at CB-2 on 5.xi.1990. This specimen is illustrated in Figs. 5-6.



FIGS. 5-6. *Eurema nise nise* (Cramer), ♂, upper (5) and under (6) surfaces: CAYMAN BRAC I[SLAND]: South Side road from Jennifer Bay to Pollard Bay; Sta. CB-2; 5.xi.1990 (S. R. Steinhauser & Z. M. Schwendeman); Allyn Museum photographs 911105-23/25. Scale line = 10 mm.

Papilionidae

Heracles andraemon andraemon (Huebner, 1823): The nominate subspecies, described from Cuba, is restricted to Cayman Brac and Little Cayman; specimens were collected at CB-2 (4-5.xi.1990), CB-3 (6.xi.1990), and CB-6 (6.xi.1990). These are comparable to Cuban specimens.

Heracles andraemon tailori (Rothschild and Jordan, 1906): A single specimen of this Grand Cayman endemic was collected at GC-2 on 31.x.1990.

Hesperiidae

Urbanus proteus domingo (Scudder, 1872): This was the commonest skipper in the collections from the Caymans, specimens were collected at GC-2 (31.x.1990), CB-2 (4.xi.1990), CB-3 (4.xi.1990), and CB-6 (6-7.xi.1990).

Urbanus dorantes santiago (Lucas, 1857): This Cuban endemic subspecies was rep-



FIGS. 7-8: *Urbanus dorantes santiago* (Lucas), ♀, upper (7) and under (8) surfaces: GRAND CAYMAN I[SLAND]: Great Beach, N of quarry; Sta. GC-3; 2.xi.1990 (S. R. Steinhauser & Z. M. Schwendeman) Allyn Museum photographs 911106-1/3. Scale line = 10 mm.

resented in the collection by a single female from GC-3 (2.xi.1990). It previously is unrecorded from the Caymans, although Schwartz et al. (1987: 147) record the Hispaniolan subspecies, *cramptoni* (Comstock, 1944). Comparison of the single Cayman specimen, which we illustrate (Figs. 7-8), with long series from Hispaniola and Cuba reveals the close affinity of the latter to the Cayman specimen.

Cybaeus tripunctus tripunctus (Herrich-Schaeffer, 1865): This butterfly was captured only at station CB-6, 6-7.xi.1990, but it was locally common. It previously has been reported from both islands under consideration here.

Hylephila phyleus phyleus (Drury, 1773): Although it has been reported from Grand Cayman and Cayman Brac (Schwartz et al. 1987: 147), specimens were procured only at GC-2 (31.x.1990) and GC-4 (1.xi.1990) during this trip.

Panoquina sylvicola (Herrich-Schaeffer, 1865): Previously recorded from Grand Cayman, specimens of this species were captured at stations GC-2 (31.x and 2.xi.1990), GC-3 (31.x and 2.xi.1990), and GC-4 (1-3.xi.1990). *Panoquina sylvicola* remains unrecorded from the other Cayman Islands.

SUMMARY

In summary, the Cayman Islands have been populated from a number of sources, most notably Cuba and Jamaica. Carpenter and Lewis (1943) and Schwartz et al. (1987) mention cases where subspecies of butterflies from both of the larger islands are present somewhere in the Caymans, and we have seen specimens that confirm the presence of at least the two *Heraclides andraemon* populations. We cannot, however, verify that the populations of *Strymon acis* from the Caymans are of both Cuban and Jamaican subspecies; rather, all of the specimens we have examined are of the Jamaican race. Similarly, though Schwartz et al. (1987) record *Urbanus dorantes cramptoni* from Grand Cayman, the specimen that we have examined and illustrated herein is clearly *U. d. santiago* (Lucas); it is entirely possible that different invasions of that species could have arrived from different islands. We have seen no Hispaniolan elements from the Cayman fauna; instead there is a preponderance of Jamaican and Cuban taxa represented.

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A NEW SPECIES OF *COLORADIA* FROM SONORA AND CHIHUAHUA, MEXICO (SATURNIIDAE: HEMILEUCINAE)

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ABSTRACT. *Coloradia prchali*, new species, is described from the mountains of eastern Sonora and western Chihuahua, Mexico. This charcoal black species is sympatric with *Coloradia luski* and has been collected only from the region around Yecora, Sonora, Mexico, at an elevation of 1050 m to 1900 m, primarily in the pine/oak forest habitat (Petran [Madrean] Conifer Forest). It also has been collected sparingly in the oak woodland habitat (Madrean Evergreen Woodland) just below the pine/oak forest community. Females of this species are attracted to Mercury Vapor and Ultra-violet light, but only five males have been collected at light. Males are primarily day fliers and have been observed flying (and attracted to virgin females) between 0900 and 1500 h. Genitalic characters indicate that *C. prchali* is most closely related to *C. luski* but characters of the foretibia are more similar to *Coloradia pandora*.

Additional key words: Systematics, variation, distribution, habitat, Sonoran Lepidoptera Survey.

The Lepidoptera fauna of Sonora, Mexico, was poorly known until the past decade. Recent collecting efforts have increased significantly our understanding of this fauna (Holland & Forbes 1981, Friedlander 1985, Smith 1985, Opler 1986, Miller & Miller 1988, Donahue 1989, Rindge 1990). In 1982, Steve Prchal of Tucson, Arizona, began his ecological and entomological studies in the mountains and plains of Sonora. The successes of his early trips sparked the interests of several other Arizonan collectors and resulted in annual collecting trips into various parts of Sonora. A result of these expeditions has been a dramatic increase in the number of Lepidoptera recorded from northwestern Mexico, including saturniid moths (Saturniidae). Hoffmann (1942) recorded only six species of saturniids from Sonora. There are now 37 species of Saturniidae documented and another 5 to 10 species are considered possible from this Mexican state (M. Smith, unpubl. data). Many of these species have proven to be significant range extensions for Mexican Saturniidae, including *Rothschildia orizaba orizaba* (Westwood), *Antheraea montezuma* (Sallé), *Copaxa muellerana* (Dyar), *Automeris boudinotiana* Lemaire, *Automeris metzli* (Sallé), *Anisota assimilis* Druce, *Sysphinx colloida* (Dyar), *Citheronia beledonon* Dyar,

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and *Dysdaemonia boreas* (Cramer). Certainly one of the most interesting discoveries was an undescribed charcoal-black, white-fringed *Coloradia* (Hemileucinae). Collecting efforts in 1988 through 1991 provided a number of specimens for study.

***Coloradia prchali* Lemaire & M. J. Smith, new species**
(Figs. 1A & B, 2; Plate 1A & B)

Male. *Head:* Black, scattered with whitish scales; labial palpi two-segmented, about the same color as the frontal area. Antennae quadripectinate to the apex, flagellum rusty yellow, rami black; apical rami shorter than basal rami, those of outer side less than half as long as those of inner side of flagellum. *Thorax:* Dorsally covered with black hairs, speckled with white hairs, the latter most prevalent on the metathorax. Legs dark brown with intermixed black and white hairs; foretibia (Fig. 1C, D) lacking the epiphysis in the dissected specimens ($n = 4$) but bearing a long spine arising from the inner apical angle. *Abdomen:* Black, the white scales not abundant dorsally and ventrally but laterally forming well defined streaks. *Forewing:* Length 28.1–31.0 mm ($\bar{x} = 29.4$ mm, $n = 12$). Above charcoal black, slightly and irregularly suffused with white scales; the overscaling most prevalent on the anterior half of the costa, the medial area and the outer side of the almost obsolescent postmedian line. The latter and the black rounded discal spot are all that remain of the ornamentation, except for small but contrasting white dots of the fringes at the apex of veins A to R5. Forewing below as dorsally with the whitish overscaling much reduced and restricted to the postmedian area. *Hindwing:* Above and below entirely black, with a slightly darker rounded discal spot; the pure white fringes contrasting well on both sides of the wing.

Female. *Head:* Same as male except antennae yellow, strongly bidentate to the apex. *Thorax and abdomen:* Same as male, except usually a more conspicuous speckling of white hairs on the dorsum of the abdomen. *Forewing and hindwing:* Same ground color and markings as in male, except usually with less white speckling on the upper forewings. Forewing length: 35.7–41.9 mm ($\bar{x} = 39.0$ mm, $n = 22$), about one-third larger than the male.

Variation. Wing pattern elements and other structures appear to be consistent. Variation is restricted to the degree of whitish overscaling on the upper surface of the forewings of both sexes. Sexual dimorphism is negligible and is restricted to smaller overall size of males.

Male genitalia (Fig. 2A, B). Uncus down-curved, simple but apically bidentate, dorsally crowned by a broad subsclerotic protuberance, rising from the posterior edge of the tegumen, characteristic of the genus. Valves bilobed, transtilla with a narrow but strongly sclerotic medial plate laterally connected both to the anterior portion of the costal lobe of the valves and the posterior area of the tegumen. Juxta very narrow, laterally connected by a membrane to the base of the sacculus lobe of the valves. Saccus broad, anteriorly rounded. Aedeagus small, slightly sinuous.

Female genitalia (Fig. 2C). Sclerotization of the eighth sternum circumvaginal with a broad membranous subtriangular medial area and laterally separated from the eighth tergum by a narrow membranous gap. Eighth tergum bilobed, subsclerotic. Postapophyses about one-fourth longer than the anapophyses. Ductus bursae membranous; bursa short, not bulky; ductus seminalis rising from the right hand side of base of bursa. Oviporus well developed, covered with relatively strong setae.

Types. *Holotype:* male, Mexico, Sonora, 11.2 km NW of Yecora, off old Santa Rosa to Yecora road, 1550 m, 2/4 July 1989 (*leg.* M. Lindberg). *Allotype:* female, same data as holotype. *Paratypes:* 15 males, 41 females, data as follows: 1 male, 11 females, same data as holotype; 1 male, 2 females, same locality as holotype, 3 July 1989 (*leg.* K. Koppes); 1 female, same locality as holotype, 3 July 1988 (*leg.* M. Lindberg); 2 females, same locality as holotype, 3 July 1989 (*leg.* R. Nagle); 3 females, same locality as holotype, 1/3 July 1989 (*leg.* M. Wilson); 9 females, same locality as holotype, 28/29 June 1990 (*leg.*

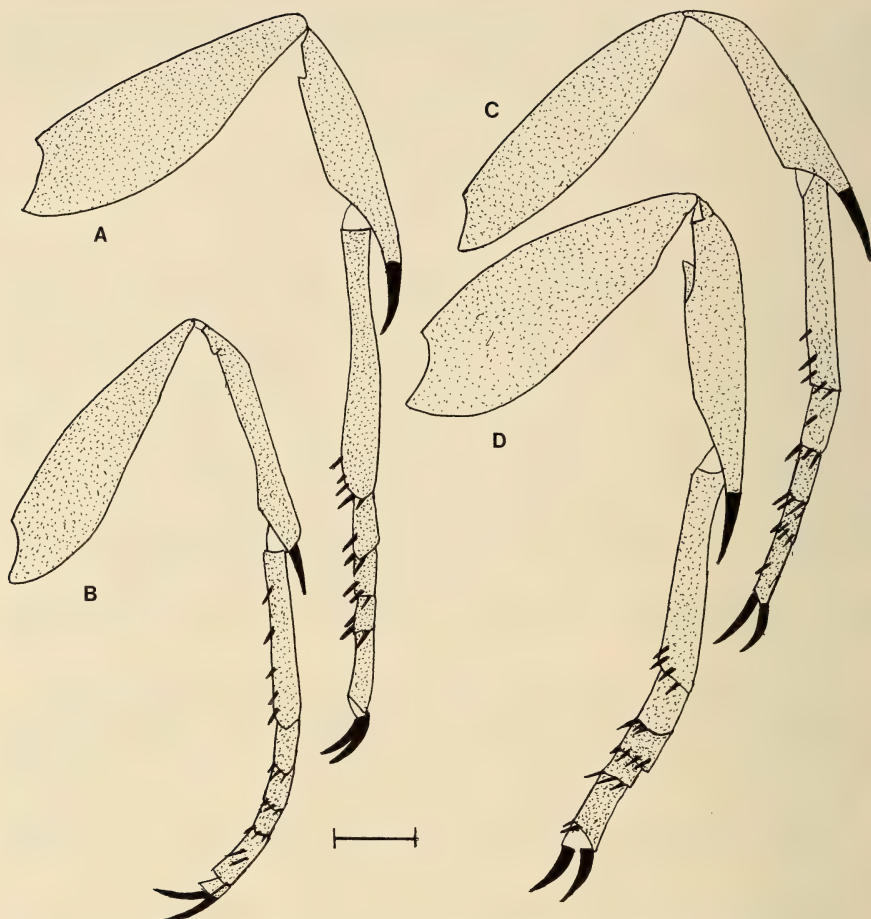


FIG. 1. Forelegs of *Coloradia*: A) *C. pandora davisi* male; B) *C. luski* male; C) *C. prchali* male; D) *C. prchali* female. Scale line = 1 mm.

M. Smith); 2 females, same locality as holotype, 28/29 June 1990 (*leg.* D. Mullins); 2 females, same locality as holotype, 28/29 June 1990 (*leg.* K. Hansen); 1 male, same locality as holotype, 28/29 June 1990 (*leg.* M. Lindberg); 1 male, same locality as holotype, 1/3 July 1989 (*leg.* J. Palting); 1 female, 4.0 km east of Santa Rosa, old Santa Rosa-Yecora road, 1040 m, 11/12 August 1983 (*leg.* S. Prchal); 1 female, 3.2 km south of La Trinidad mine, off old Santa Rosa-Yecora road, 1200 m, 28 July 1987 (*leg.* P. Jump); 11 males, 7 females, 9.6 km WSW of Yecora, Hwy 16, 1600 m, 7 July 1991 (*leg.* J. Brock & S. Prchal).

Disposition of types. The holotype male and allotype female have been deposited in the Natural History Museum of Los Angeles County, Los Angeles, California. One paratype pair has been deposited in the Muséum national d'Histoire naturelle, Paris, France; two paratype pairs have been deposited in the Sonoran Arthropod Studies, Inc. (SASI) collection, Tucson, Arizona. Two paratype pairs have been deposited in the UNAM collections: Instituto de Biología, Mexico, D.F., Mexico and Museo de Zoología, Mexico, D.F., Mexico. Paratype pairs have been deposited in the collections of the following institutions: Natural History Museum of Los Angeles County, Los Angeles, California;

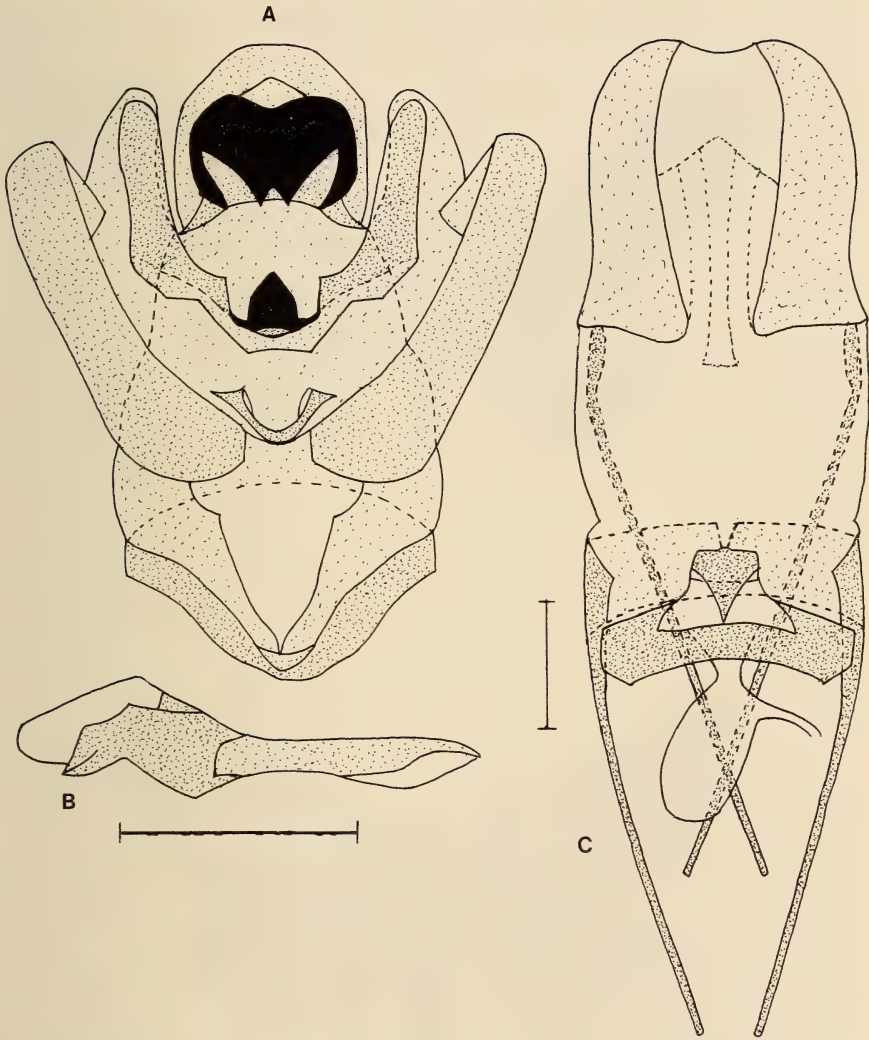


FIG. 2. Male genitalia of *Coloradia prchali* new species: A) Ventral view, aedeagus removed; B) Lateral view of aedeagus. C) Female genitalia of *Coloradia prchali* new species. Scale line = 1 mm.

California Academy of Sciences, San Francisco, California; United States National Museum (Smithsonian Institution), Washington, D.C.; and American Museum of Natural History, New York, New York. Other paratypes will remain in the collections of the original collectors and of the junior author.

Diagnosis. *Coloradia prchali* differs from previously described *Coloradia* species by its darker coloration, extreme reduction of ornamentation, and complete absence of red scales from the body as well

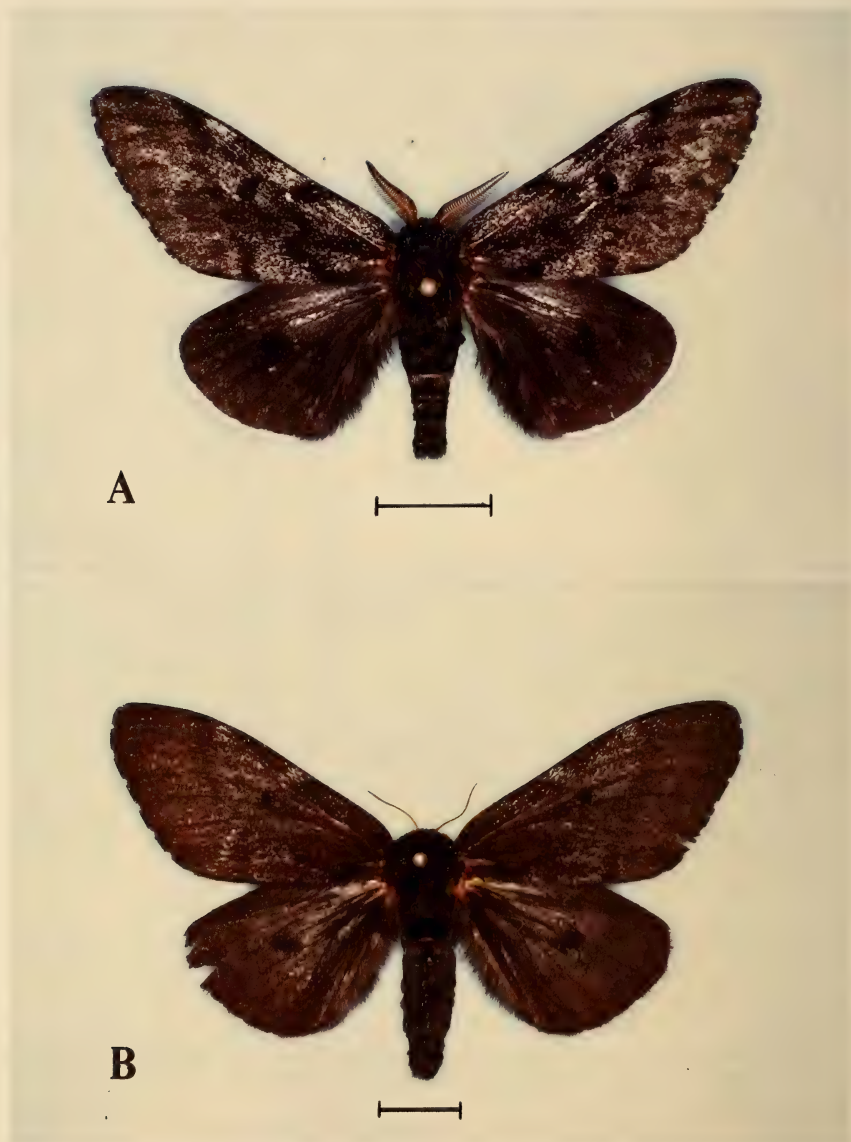


PLATE 1. *Coloradia prchali*, new species. A) Male holotype, Mexico, Sonora, 11.2 km NW of Yecora, off of Santa Rosa road, 1550 m, 2/4 July 1989 (leg. M. Lindberg). B) Female allotype, same data as holotype. Scale line = 10 mm.



FIG. 3. Distribution of *Coloradia prchali* (●) in northwestern Mexico.

as from the hind wing. *Coloradia prchali* appears more closely related to *Coloradia luski* Barnes and Benjamin than to any other form of *Coloradia*. The wing pattern elements in both sexes are most similar to that of dark females of *C. luski* (see Ferguson 1971: pl. 6, fig. 13). However, *C. luski* never has the charcoal black color as on *C. prchali*. *Coloradia prchali* also differs from *C. luski* by its absence of sexual

dimorphism in color and pattern and the lack of individual variation; whereas *C. luski* is probably the most variable species in *Coloradia* (Ferguson 1971; Lemaire, pers. obs.). *Coloradia prchali* is larger than *C. luski* in both sexes: *Coloradia prchali* males, \bar{x} = 29.4 mm, n = 12; *C. luski* males, \bar{x} = 26.5 mm, n = 12; *Coloradia prchali* females, \bar{x} = 39.0 mm, n = 22; *C. luski* females, \bar{x} = 30.6 mm, n = 2). The two species also are differentiated by the coloration of the rami in the male antennae, black in *C. prchali* and yellow in *C. luski*. Male specimens of *C. prchali* fly during the daytime (J. Brock & S. Prchal, pers. comm.), a unique habit within the genus. The foretibial spine (Fig. 1) is noticeably longer in relation to the tibia in *C. prchali* than in *C. luski* (24 percent vs. 16.7 percent). It is about the same percentage in *C. prchali* and *C. pandora davisii* Barnes & Benjamin (see Ferguson 1971). The small differences between the genitalia of *C. prchali* and *C. luski*, such as the absence of the notch at the apex of the dorsal protuberance of the uncus and the larger medial plate of the transtilla, require larger series of dissections to be analyzed for significance.

Etymology. This species is named in honor of Steve Prchal, who captured the first specimen of this saturniid and whose enthusiastic interests in Sonora sparked the collecting efforts of many others over the past decade.

Distribution (Fig. 3). All known specimens of *C. prchali* have been collected in the mountainous region around Yecora, in eastern Sonora, Mexico. This distribution includes western Chihuahua and is in the Sierra Madre Occidental mountains of northwestern Mexico. The type locality, located in the Petran (Madrean) Conifer Forest habitat of Brown (1982), is a plateau region northwest of Yecora at about 1550 m. Most of the known specimens of *C. prchali* have been collected in this habitat, which is community of pine/oak trees, some shrubs, and grasslands, including various conifer species as *Pinus ponderosa* Lawson, *P. engelmannii* Carr. [= *P. latifolia* Sarg.], and *P. leiophylla* var. *chihuahuana* Engelm. (all Pinaceae); *Juniperus deppeana* Steud. (Cupressaceae); and various evergreen oaks, including *Q. pennivenia* Trel., *Q. arizonica* Sarg., *Q. grisea* Liebm., *Q. viminea* Trel., and *Q. fulva* Lieb. (Fagaceae). Within this habitat, *C. prchali* also has been recorded from 6.4 km east-northeast of Yecora and from 9.6 km south of Yecora by P. Jump and S. McCleve. This latter locality is in Chihuahua, Mexico, and thus documents *C. prchali* for this Mexican state. *Coloradia prchali* also was recorded from 13.6 km west-southwest of Yecora at 1900 m by D. Mullins and B. Kelly. The latter locality is a more mixed chaparral habitat within the Petran (Madrean) Conifer Forest community.

Outside of this habitat community, one female paratype was collected

in the Madrean Evergreen Woodland habitat south of La Trinidad mine, a region of steep canyons (barrancas) and ridges that is primarily oak woodland with associated pine and juniper species, and several shrubs such as *Ceanothus* (Rhamnaceae) and *Arbutus* (Ericaceae). Another paratype female (actually the first known specimen of this species) was collected in Sinaloan Thornscrub habitat between Santa Rosa and La Trinidad mine. However, this locality is a canyon bottom immediately below the Madrean Evergreen Woodland habitat occurring on the hills just above. The female probably strayed down from the latter habitat.

Coloradia prchali should be found in similar habitats in eastern Sonora and western Chihuahua in the Sierra Madre Occidental. *Coloradia luski* has been collected sympatrically with *C. prchali*, although the flight period of *C. luski* begins approximately two weeks later (M. Smith, unpubl. data). The surrounding Sierra Madre Occidental, east and south of the Yecora region, also supports populations of *C. pandora davis*.

Collection dates for *C. prchali* range from 28 June to 15 August, indicating a midsummer flight. The peak flight seems to be early July, coinciding with the beginning of the annual monsoon rains. Since 1983, a total of five males and over 50 females (including non-paratype females) have been collected at UV and MV light. Field studies in 1991 resulted in males being attracted to virgin female *C. prchali*, indicating that males of this species are diurnal, flying between 0900 and 1500 h (J. Brock & S. Prchal, pers. comm.). This diurnal flight habit is unusual for the genus. *Coloradia pandora lindseyi* Barnes & Benjamin was reported as a day flier by Patterson (1929); Schmid and Bennett (1988) and Brown (1984) reported *C. pandora davis* flying in the daytime during years of unusual abundance.

The larval stages of *C. prchali* have not been observed in nature; however, larvae of this species have been reared in captivity on various *Pinus* species (Pinaceae) by several workers. The life history of *C. prchali* will be the subject of a later paper by K. Wolfe of Escondido, California.

Discussion. The genus *Coloradia* Blake, 1863, with type-species *Coloradia pandora* Blake, 1863, by original designation (Fletcher & Nye 1982), occupies the western half of the United States, ranging as far north as Wyoming and South Dakota (Ferguson 1971), and south to at least Oaxaca and Chiapas in southern Mexico (K. Wolfe, pers. comm.). Four species occur in the United States: *C. pandora*, *C. doris* Barnes, *C. luski*, and *C. velda* Johnson & Walter (Ferguson 1983, Johnson & Walter 1979). Beutelspacher (1978) cited only three species from Mexico, all endemics: *C. euphrosyne* Dyar, *C. vazquezae* Beutelspacher, and *C. hoffmanni* Beutelspacher, although Hoffmann (1942) also listed

C. pandora from Sinaloa. Since the 1978 revision by Beutelspacher, *C. luski* and *C. p. davisii* have been found in northern Mexico (specimens at Univ. California Davis, in the collection of T. Sears from southwestern Chihuahua) and *C. pandora* (probably subspecies *lindseyi*) has been confirmed from Baja California Norte (Johnson & Walter 1979). This description of *Coloradia prchali* brings the number of *Coloradia* species known from Mexico to six.

ACKNOWLEDGMENTS

We thank Steve Prchal for bringing this species to our attention. We also thank the collectors who generously shared their specimens and locality data with us: Jim Brock, John Palting, Ray Nagle, Markus Lindberg, Keith Koppes, Michael Wilson, Doug Mullins, and Bob Weich, all of Tucson, Arizona; Peter Jump and Scott McCleve, Douglas, Arizona; and Ken Hansen, Eureka, California. We thank the many other collectors who have been part of the collecting trips to this region, under the loose guise of the Sonoran Lepidoptera Survey. We especially thank Jim Brock and Doug Mullins for spearheading the efforts to gather data and specimens for study. Kirby Wolfe provided field data on Mexican *Coloradia*. Steve Stone took the color photographs of the type specimens. Julian Donahue of the Natural History Museum of Los Angeles County reviewed the manuscript and offered helpful suggestions. We thank two anonymous reviewers for their comments and suggestions.

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BUTTERFLIES OF THE ARCHBOLD BIOLOGICAL STATION, HIGHLANDS COUNTY, FLORIDA

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ABSTRACT. Seventy butterfly species (27 Hesperiidae, 16 Nymphalidae, 11 Pieridae, 8 Papilionidae, and 8 Lycaenidae) have been recorded from the Archbold Biological Station near the southern end of the Lake Wales Ridge in Highlands County, Florida. Peaks of abundance and diversity for adult butterflies at Archbold occur in March and August. At least 11% (70 species) of the plants at the station provide butterflies with nectar or larval hosts, many of which are documented for the first time. Crab spiders, the green lynx spider, a phymatid bug, and a robber fly were observed feeding on adult butterflies. Approximately 12% of the butterflies found in Highlands County are limited primarily to peninsular Florida.

Additional key words: food plants, distribution, phenology, predators, Lake Wales Ridge.

The Archbold Biological Station (ABS) serves not only as a major center of biological research in Florida, but also as a preserve of the natural communities of the southern Lake Wales Ridge (Minno & Myers 1986). The Lake Wales Ridge is one of several ancient dune formations that run parallel to the peninsular coastline (Fig. 1). The deep, sandy soils of this region have given rise to distinctive xerophytic plant communities that contain many unusual organisms. Ward (1979) lists 18 endangered, threatened, and rare species of plants from the Lake Wales Ridge area. Neill (1957) discusses over 50 animal taxa found mostly in central peninsular Florida.

Fire plays an important role in shaping and maintaining the natural communities at ABS. Prescribed burning of small tracts of the station is conducted annually. Lightning-induced wildfires also occur regularly, especially during the summer. Central Florida experiences a hot, humid rainy season with frequent thunderstorms from June through September. Winters are mild and dry with occasional temperatures below freezing (Chen & Gerber 1990).

Some 540 species of vascular plants grow naturally at the station (Vander Kloet 1986), and about 80 species of exotic plants have been planted on the property (Herndon 1986). Abrahamson et al. (1984b) describe the plant associations of the station in detail. Generally, the western half of ABS is a mixture of flatwoods, scrub, and seasonal ponds. A few small bayheads (stands of broad-leaved evergreen trees), dominated by Loblolly Bay, *Gordonia lasianthus* (L.) Ellis (Theaceae), occur along the western and northern boundaries. Sand Pine scrub predominates in the northeastern portion of the station in the area around Red Hill. Sandhill vegetation covers the top of Red Hill and much of the



FIG. 1. Map of Florida showing the locations of the major sand ridges (after White 1970) and the Archbold Biological Station.

land from the main compound south to the abandoned settlement of Hicoria. A detailed vegetation map by Abrahamson, Johnson, and Layne (1984a) is available from ABS. Figure 2 shows a map of the main features of the station.

Little has been published on the butterflies of the Lake Wales Ridge.

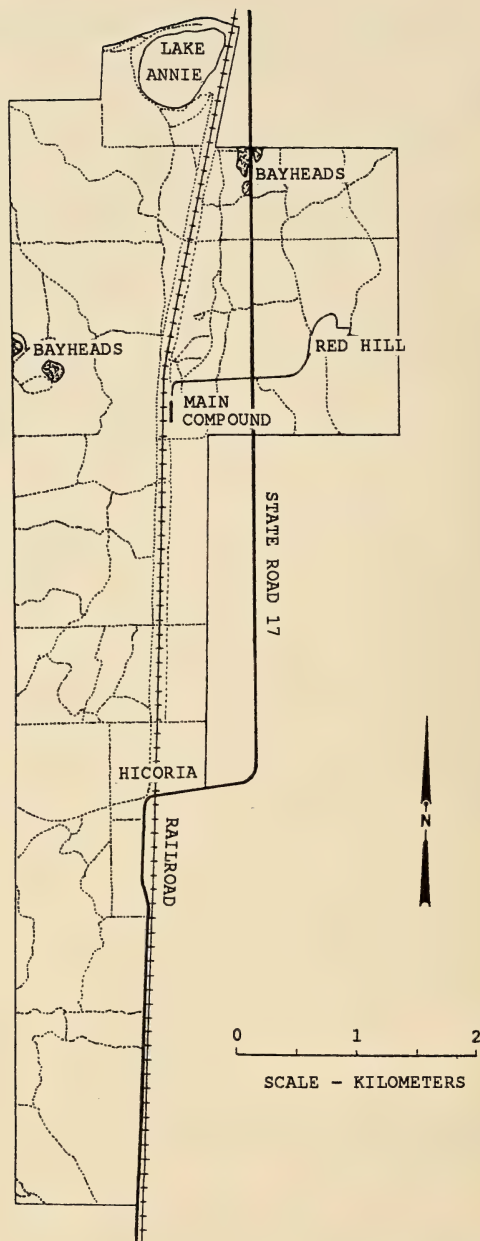


FIG. 2. Map of the Archbold Biological Station. Dotted lines indicate trails.

Comstock and Comstock (1902) listed 20 species from two sites on the ridge, Avon Park and Lake Josephine, in Highlands County. Frost (1964, 1966, 1969, 1975) collected ten species of hesperiids, five lycaenids, and two nymphalids in ultraviolet light traps at ABS. Other sources of data are mentioned in the species accounts below. In another report (Minno 1988), I presented a check list of the Lepidoptera of ABS. Here, I list the butterflies recorded from ABS and discuss their relative abundance, phenology, larval and adult resources, and predators.

METHODS

I collected and observed butterflies at ABS during November 1983; June–August, September, October, and November 1986; February and March 1987; and April 1988. During 1986 I visited nearly all parts of the station accessible by trail or road, but concentrated my efforts around the main buildings, Red Hill, Hicoria, and in the shallow ponds dominated by Redroot *Lachnanthes caroliniana* (Lam.) Dandy (Hae-modoraceae) near the western bayheads, because these areas usually had an abundance of flowers that attracted butterflies. At each site, the date, beginning and ending sampling time, weather, species and number of individuals of each species observed, flowers visited, host plants, and predators, were recorded. Voucher specimens were deposited in the ABS reference collection.

ANNOTATED LIST OF SPECIES

The butterflies of ABS are discussed individually in the following list. Where known, the status, habitat, abundance, flight period, host plants (larval food plants), nectar sources, and predators are presented. The families and subfamilies are arranged in taxonomic order according to Hodges et al. (1983). Species are listed in alphabetical order. I categorize the butterfly species as abundant if they are likely to be encountered on a field trip to ABS, occasional if they are irregularly present in low numbers, and uncommon if less than five individuals are recorded from the station. Reference to eggs, larvae, or pupae indicates that more than one immature individual was found, but exact numbers were not recorded. The plant taxonomy and nomenclature used in the paper conforms primarily to that of Wunderlin (1982).

HESPERIIDAE: PYRGINAE

Epargyreus clarus clarus (Cramer)

STATUS: Occasional in the old citrus grove on Red Hill.

HOST PLANTS: One larva was found on *Galactia regularis* (L.) BSP. (Fabaceae).

FLOWERS VISITED: *Lantana camara* L. (Verbenaceae).

Erynnis brizo somnus (Lintner)

STATUS: Abundant in Sand Pine scrub, sandhill, and scrubby flatwoods habitats during the spring. Frost (1975) took one in an ultraviolet light trap.

HOST PLANTS: Larvae were found on *Quercus inopina* Ashe and *Quercus myrtifolia* Willd. (Fagaceae).

FLOWERS VISITED: *Conradina canescens* (Torr. & Gray) A. Gray (Lamiaceae).

Erynnis horatius (Scudder & Burgess)

STATUS: Abundant in Sand Pine scrub, sandhill, and scrubby flatwoods habitats. Frost (1966) took one in an ultraviolet light trap.

HOST PLANTS: Larvae were found on *Quercus inopina*, *Quercus myrtifolia*, and *Quercus hemisphaerica* Bartr. (Fagaceae).

FLOWERS VISITED: *Asclepias curtissii* A. Gray (Asclepiadaceae), *Bidens alba* (L.) DC. (Asteraceae), *Balduina angustifolia* (Pursh) Robins. (Asteraceae), *Dalea feayi* (Chapm.) Barneby (Fabaceae), *Diodia teres* Walt. (Rubiaceae), *Heterotheca subaxillaris* (Lam.) Britt. and Rusby (Asteraceae), *Lachnanthes carolinianum*, *Lantana camara*, *Palafoxia feayi* A. Gray (Asteraceae), *Vernonia gigantea* (Walt.) Trel. ex Branner and Coville (Asteraceae), *Wedelia trilobata* (L.) Hitchc. (Asteraceae). Males were occasionally found at mud puddles.

PREDATOR: An unidentified crab spider (Thomisidae) was found feeding on an adult on *Lachnanthes*.

Erynnis juvenalis juvenalis (Fabricius)

STATUS: Abundant in Sand Pine scrub, sandhill, and scrubby flatwoods habitats during the spring. One adult was taken in July (Burns 1964). Frost (1975) collected one in an ultraviolet light trap.

HOST PLANTS: A larva was found on *Quercus inopina* at Highlands Hammock State Park.

Erynnis zarucco zarucco (Lucas)

STATUS: Abundant in Sand Pine scrub, sandhill, scrubby flatwoods and disturbed sites. Frost (1969) took a few in an ultraviolet light trap.

HOST PLANTS: Larvae were found on *Galactia elliottii* Nutt. (Fabaceae), *Galactia regularis*, and *Indigofera caroliniana* Mill. (Fabaceae).

FLOWERS VISITED: *Asclepias curtissii*, *Bidens alba*, *Dalea feayi*, *Heterotheca subaxillaris*, *Lachnanthes caroliniana*, *Lantana camara*, *Liatris tenuifolia* Nutt. (Asteraceae).

PREDATOR: A green lynx spider (*Peucetia viridans* Hentz; Oxyopidae) was found feeding on an adult on *Lachnanthes*.

Pyrgus oileus oileus (Linnaeus)

STATUS: Uncommon in scrubby flatwoods and disturbed sites. One was taken in a Malaise trap in Sand Pine scrub by M. Deyrup (ABS reference collection). The dry season phenotype, *montivagus*, begins to appear in November.

Thorybes pylades (Scudder)

STATUS: Occasional in sandhill and scrubby flatwoods habitats. Frost (1975) took one in an ultraviolet light trap.

HOST PLANTS: Larvae were found on *Galactia regularis* and *Rhyncosia difformis* (Ell.) DC. (Fabaceae).

FLOWERS VISITED: *Asclepias curtissii*, *Bidens alba*, *Lantana camara*, *Lachnanthes carolinianum*.

PREDATOR: A *Phymata guerini* Lethierry & Severin (Hemiptera: Phymatidae) caught an adult at flowers (ABS reference collection).

Urbanus dorantes dorantes (Stoll)

STATUS: The Dorantes Skipper became established in Florida sometime in the late 1960's (Clench 1970). Knudson (1974) found this species to be abundant on 12 October 1972 near Bartow in Polk County. The Dorantes Skipper was abundant in the old citrus grove on Red Hill and occasional in scrubby flatwoods during the summer of 1986.

HOST PLANTS: Observed ovipositing on *Desmodium incanum* DC. (Fabaceae).

FLOWERS VISITED: *Bidens alba*, *Lachnanthes carolinianum*, *Lantana camara*, *Richardia scabra* L. (Rubiaceae), *Satureja rigida* Bartr. ex Benth. (Lamiaceae).

Urbanus proteus proteus (Linnaeus)

STATUS: Abundant during the fall when dispersing adults fly southward through Florida in large numbers. Frost (1969) captured a few in an ultraviolet light trap.

HOST PLANTS: Larvae were found on *Centrosema floridanum* (Britt.) Lakela, *Desmodium incanum*, *Desmodium tortuosum* (Sw.) DC., and *Vigna luteola* (Jacq.) Benth. (all Fabaceae).

FLOWERS VISITED: *Bidens alba*, *Crotalaria mucronata* Desv. (Fabaceae), *Lachnanthes carolinianum*, *Lantana camara*, *Liatris tenuifolia*, *Satureja rigida*, *Urena lobata* L. (Malvaceae).

HESPERIIDAE: HESPERIINAE

Ancyloxypha numitor (Fabricius)

STATUS: Uncommon and local in the ditches bordering the railroad tracks. Although numerous seasonal ponds occur within the flatwoods at ABS, *A. numitor* does not utilize these areas, perhaps due to the lack of suitable larval food plants. The Least Skipper is often closely associated with *Leersia* spp. (Poaceae) and other semi-aquatic grasses in Florida.

Asbolis capucinus (Lucas)

STATUS: Uncommon on the top of Red Hill and on the main grounds.

HOST PLANTS: One larva was found on *Sabal etonia* Swingle ex Nash (Arecaceae).

FLOWERS VISITED: *Ipomoea cairica* (L.) Sweet (Convolvulaceae).

Atalopedes campestris huron (Edwards)

STATUS: Occasional in scrubby flatwoods and disturbed sites. Frost (1975) took a few in an ultraviolet light trap.

FLOWERS VISITED: *Dalea feayi*, *Lachnanthes carolinianum*, *Lantana camara*.

Atrytone delaware delaware (Edwards)

STATUS: Occasional in scrubby flatwoods.

HOST PLANTS: Larvae were found on *Panicum hemitomon* Schult. (Poaceae).

FLOWERS VISITED: *Dalea feayi*, *Ipomoea cairica*, *Lachnanthes carolinianum*, *Lantana camara*, *Liatris ohlingerae* (Blake) Robins. (Asteraceae), *Liatris tenuifolia*.

Atrytonopsis hianna loammi (Whitney)

STATUS: R. W. Pease Jr. collected three adults at ABS on 16, 24, and 27 September 1960 (ABS reference collection). This species should occur in the scrubby flatwoods areas of the station, but I did not find it.

Copaeodes minimus (Edwards)

STATUS: Occasional in the old citrus grove on Red Hill and in scrubby flatwoods.

FLOWERS VISITED: *Dalea feayi*, *Heterotheca subaxillaris*, *Lachnanthes caroliniana*.

Euphyes arpa (Boisduval & Leconte)

STATUS: Abundant in scrubby flatwoods during the late summer and fall.

HOST PLANTS: Larvae were found on *Sabal etonia* and *Serenoa repens* (Bartr.) Small (Arecaceae).

FLOWERS VISITED: *Asclepias* species, *Lachnanthes carolinianum*, *Liatris tenuifolia*, *Palafoxia feayi*.

PREDATOR: An unidentified crab spider (Thomisidae) was found feeding on an adult on *Liatris*.

Hesperia meskei straton (Edwards)

STATUS: R. W. Pease Jr. collected one on 10 October 1960 at ABS (reference collection). I did not find *H. meskei* in the fall of 1986, but it should occur in the sandhill and scrubby flatwood areas of the station.

Hylephila phyleus phyleus (Drury)

STATUS: Abundant in sandhill, scrubby flatwoods, and disturbed areas. Frost (1975) took one in an ultraviolet light trap.

HOST PLANTS: Observed ovipositing on *Stenotaphrum secundatum* (Walt.) Kuntze (Poaceae).

FLOWERS VISITED: *Asclepias curtissii*, *Dalea feayi*, *Lachnanthes carolinianum*, *Lantana camara*, *Liatris tenuifolia*, *Satureja rigida*.

PREDATORS: Green lynx spider (*Peucetia viridans*), an unidentified crab spider (Thomisidae), *Phymata guerini* (Hemiptera: Phymatidae), all on *Lachnanthes*, and a large gray robber fly (Diptera: Asilidae).

Lerema accius accius (J. E. Smith)

STATUS: Uncommon in the old citrus grove on Red Hill and on the main grounds. Frost (1975) took a few in an ultraviolet light trap.

FLOWERS VISITED: *Bidens alba*, *Ipomoea cairica*, *Lantana camara*.

Lerodea eufala eufala (Edwards)

STATUS: Occasional in scrubby flatwoods.

FLOWERS VISITED: *Lachnanthes caroliniana*, *Richardia scabra*.

Nastra lherminier (Latreille)

STATUS: Uncommon in scrubby flatwoods. One was collected in a Malaise trap in Sand Pine scrub by M. Deyrup (ABS reference collection).

Oligoria maculata (Edwards)

STATUS: Occasional in scrubby flatwoods and disturbed sites.

FLOWERS VISITED: *Cirsium nuttallii* DC. (Asteraceae), *Ipomoea cairica*, *Lachnanthes caroliniana*, *Lantana camara*, *Liatris tenuifolia*, *Urena lobata*.

Panoquina ocola ocola (Edwards)

STATUS: Abundant during the fall when dispersing adults fly southward through Florida in large numbers. Frost (1966) took a few in an ultraviolet light trap.

HOST PLANTS: Observed ovipositing on *Panicum repens* L. (Poaceae).

FLOWERS VISITED: *Asclepias curtissii*, *Bidens alba*, *Balduina angustifolia*, *Dalea feayi*, *Heterotheca subaxillaris*, *Lachnanthes caroliniana*, *Lantana camara*, *Liatris tenuifolia*, *Palafoxia feayi*, *Wedelia trilobata*.

Polites themistocles (Latreille)

STATUS: Occasional in scrubby flatwoods. Frost (1975) took one in an ultraviolet light trap.

HOST PLANTS: Observed ovipositing on *Panicum aciculare* Desv. ex Poir. (Poaceae).

FLOWERS VISITED: *Lachnanthes carolinianum*.

Polites vibex vibex (Geyer)

STATUS: Abundant in sandhill, scrubby flatwoods, and disturbed areas. Frost (1969) captured one in an ultraviolet light trap.

FLOWERS VISITED: *Asclepias curtissii*, *Bidens alba*, *Dalea feayi*, *Diodia teres*, *Lachnanthes carolinianum*, *Lantana camara*, *Liatris tenuifolia*, *Momordica charantia* L. (Cucurbitaceae), *Satureja rigida*, *Vernonia gigantea*.

Wallengrenia otho (J. E. Smith)

STATUS: Occasional in scrubby flatwoods and disturbed sites.

FLOWERS VISITED: *Asclepias curtissii*, *Lachnanthes carolinianum*, *Lantana camara*.

HESPERIIDAE: MEGATHYMINAE

Megathymus yuccae buchholzi H. A. Freeman

STATUS: Although adults were seen infrequently, immatures were abundant on Red Hill and in scrubby flatwoods during 1986 and 1987. Males perched on the ground or low vegetation in open areas at mid-day. Late-instar larvae began to develop wax glands and finished feeding in October and November.

HOST PLANTS: Ova and larvae were found on *Yucca aloifolia* L. and *Yucca filamentosa* L. (Agavaceae).

PAPILIONIDAE: PAPILIONINAE

Battus philenor philenor (Linnaeus)

STATUS: Uncommon in sandhill and scrubby flatwoods habitats.

HOST PLANTS: No native *Aristolochia* species (Aristolochiaceae) have been found at ABS (Vander Kloet 1986), and the Pipevine Swallowtail does not seem to utilize the exotic *Aristolochia littoralis* Parodi naturalized on the main grounds of the station. The few adults taken may represent strays from the Highlands Hammock area, where breeding populations are present.

Battus polydamas lucayus (Rothschild & Jordan)

STATUS: Often abundant during the fall, but local near patches of the larval food plant on the main grounds.

HOST PLANTS: Larvae were abundant on *Aristolochia littoralis* during the fall.

FLOWERS VISITED: *Clerodendrum speciosissimum* Van Geert (Verbenaceae), *Salvia coccinea* Buchoz. ex Etling (Lamiaceae).

Eurytides marcellus floridensis (Holland)

STATUS: Abundant in Sand Pine scrub, sandhill, and scrubby flatwoods habitats.

HOST PLANTS: One larva was found on *Asimina obovata* (Willd.) Nash (Annonaceae).

FLOWERS VISITED: *Lachnanthes carolinianum*.

Papilio crespontes Cramer

STATUS: Often abundant but local near citrus on Red Hill and the main grounds.

HOST PLANTS: Observed ovipositing on *Citrus* sp. (Rutaceae).

FLOWERS VISITED: *Cirsium nuttallii*, *Clerodendrum speciosissimum*, *Lantana camara*, *Palafoxia feayi*, *Salvia coccinea*, *Urena lobata*.

Papilio glaucus australis Maynard

STATUS: Occasional on Red Hill and the main grounds.

FLOWERS VISITED: *Cirsium nuttallii*, *Lantana camara*, *Urena lobata*.

Papilio palamedes Drury

STATUS: Abundant in scrubby flatwoods and other habitats.

FLOWERS VISITED: *Befaria racemosa* Vent. (Ericaceae), *Cirsium nuttallii*, *Clerodendrum speciosissimum*, *Lachnanthes carolinianum*, *Lantana camara*, *Salvia coccinea*.

Papilio polyxenes asterius Stoll

STATUS: Uncommon in scrubby flatwoods and disturbed sites.

HOST PLANTS: Observed ovipositing on *Ptilimnium capillaceum* (Michx.) Raf. (Apiaceae). Larvae and pupae were found on *Eryngium cuneifolium* Small (Apiaceae).

FLOWERS VISITED: *Lachnanthes carolinianum*.

Papilio troilus ilioneus J. E. Smith

STATUS: Abundant in scrubby flatwoods and on the main grounds.

HOST PLANTS: Larvae were found on *Persea borbonia* (L.) Spreng. (Lauraceae).

FLOWERS VISITED: *Clerodendrum speciosissimum*, *Lachnanthes carolinianum*, *Lantana camara*.

PIERIDAE: PIERINAE

Ascia monuste phileta (Fabricius)

STATUS: Abundant during early summer in the old citrus grove on Red Hill. Occasional in other habitats.

FLOWERS VISITED: *Polygala rugelii* Shuttlew. (Polygalaceae).

Pontia protodice (Boisduval & Leconte)

STATUS: Abundant in the citrus grove on Red Hill during early summer. Occasional in other habitats.

HOST PLANTS: Observed ovipositing on *Lepidium virginicum* L. (Brassicaceae).

FLOWERS VISITED: *Salvia coccinea*.

PIERIDAE: COLIADINAE

Colias eurytheme Boisduval

STATUS: Uncommon in scrubby flatwoods.

FLOWERS VISITED: *Lachnanthes carolinianum*, *Liatris tenuifolia*.

Eurema दौरा दौरा (Godart)

STATUS: Abundant during the fall when dispersing adults fly southward through Florida in large numbers.

HOST PLANTS: Observed ovipositing on *Aeschynomene americana* L. (Fabaceae) and *Indigofera hirsuta* Harv. (Fabaceae) just south of ABS at Venus.

FLOWERS VISITED: *Bidens alba*, *Dalea feayi*, *Elephantopus elatus* Bertol. (Asteraceae), *Eryngium cuneifolium*, *Galactia regularis*, *Heterotheca subaxillaris*, *Lachnanthes carolinianum*, *Liatris tenuifolia*, *Lippia nodiflora* (L.) Michx. (Verbenaceae), *Momordica charantia*, *Palafoxia feayi*, *Pityopsis graminifolia* (Michx.) Nutt. (Asteraceae), *Polygonella robusta* (Small) Horton (Polygonaceae), *Richardia scabra*, *Wedelia trilobata*. Adults also sip water from wet soil occasionally.

Eurema lisa lisa Boisduval and Leconte

STATUS: Abundant but often rather local near the larval food plant in Sand Pine scrub, sandhill, and scrubby flatwoods habitats. The winter form, which has reduced black borders on the upperside of the hindwings, begins to appear in November.

HOST PLANTS: Observed ovipositing on *Cassia fasciculata* (Michx.) Greene (Fabaceae).

FLOWERS VISITED: *Dalea feayi*, *Galactia regularis*, *Richardia scabra*, *Satureja rigida*.

Eurema nicippe (Cramer)

STATUS: Abundant in the vicinity of the larval host plant along a firelane at Hicoria. Occasional in other habitats.

HOST PLANTS: Larvae were found on *Cassia occidentalis* L. (Fabaceae).

Nathalis iole Boisduval

STATUS: Apparently abundant in disturbed sites some years. Rutowski (1981) studied the mating behavior of *N. iole* at ABS from July to November 1981. He commented that this species "flies all year" at the station. I did not find the Dainty Sulfur during any of my surveys at ABS.

Phoebis agarithe maxima (Neumoegen)

STATUS: An uncommon vagrant from south Florida. One specimen in the reference collection was taken on 28 July 1967 at ABS.

Phoebis philea philea (Johansson)

STATUS: On 5 August 1966, T. E. Pliske captured a female of this species at ABS (reference collection). *Phoebis philea* breeds in residential areas of Highlands County where ornamental species of *Cassia* have been planted (H. D. Baggett pers. comm.).

Phoebis sennae eubule (Linnaeus)

STATUS: Abundant during the fall when dispersing adults fly southward through Florida in large numbers. Of 10 individuals observed on 8 February 1987, all were flying north.

HOST PLANTS: Observed ovipositing on *Cassia fasciculata*. Larvae were found on *Cassia occidentalis*.

FLOWERS VISITED: *Bidens alba*, *Clerodendrum speciosissimum*, *Lachnanthes carolinianum*, *Lantana camara*, *Liatris ohlingerae*, *Liatris tenuifolia*, *Richardia scabra*, *Salvia coccinea*.

Zerene cesonia (Stoll)

STATUS: Uncommon in scrubby flatwoods.

FLOWERS VISITED: *Asclepias tuberosa* ssp. *rolfsii* (Britt.) Woods. (Asclepiadaceae), *Lachnanthes caroliniana*.

LYCAENIDAE: EUMAEINAE

Atlides halesus halesus (Cramer)

STATUS: Uncommon in sandhill habitats. Frost (1969) captured one in an ultraviolet light trap.

HOST PLANTS: Hatched egg shells, probably of this species, were found on *Phoradendron serotinum* (Raf.) M. C. Johnst. (Loranthaceae) growing on *Quercus myrtifolia* and *Quercus geminata* Willd. (Fagaceae).

Calycopis cecrops (Fabricius)

STATUS: Abundant in Sand Pine scrub, sandhill, scrubby flatwoods and on the main grounds. Frost (1969) took one in an ultraviolet light trap. Males hilltop in trees of various sizes. Dozens were frequently seen perching and chasing each other in the large laurel oaks planted on the main grounds during July and August. I have also observed males hilltopping on scrub oaks less than three meters tall. Hilltopping adults were especially active late in the afternoon and also on cloudy days.

HOST PLANTS: Associated with oaks (*Quercus myrtifolia*, *Quercus chapmannii* Sarg., and *Quercus hemisphaerica*) and mango (*Mangifera indica* L., Anacardiaceae). Larvae from a single female grew most rapidly on shoots and young leaves of mango, and more slowly on those of *Rhus copallina* L. (Anacardiaceae), *Q. hemisphaerica*, and *Toxicodendron radicans* (L.) Kuntze (Anacardiaceae).

FLOWERS VISITED: *Asclepias curtissii*, *Bidens alba*, *Dalea feayi*, *Gelsemium sempervirens* (L.) J. St. Hil. (Loganiaceae), *Lachnanthes carolinianum*, *Lantana camara*, *Solidago* sp. (Asteraceae).

Euristrymon favonius (J. E. Smith)

STATUS: Abundant in late spring and early summer in Sand Pine scrub, scrubby flatwoods, and on the main grounds. Frost (1975) took one in an ultraviolet light trap. Adults are associated with oaks.

FLOWERS VISITED: *Asclepias curtissii*, *Persea humilis* Nash (Lauraceae).

Parrhasius m-album (Boisduval & Leconte)

STATUS: Uncommon in scrubby flatwoods and on the main grounds. Frost (1975) captured a few in an ultraviolet light trap. Adults are associated with oaks.

FLOWERS VISITED: *Bidens alba*, *Lachnanthes carolinianum*, *Sabal etonia*.

Satyrium calanus calanus (Hübner)

STATUS: Two individuals were collected by R. W. Pease Jr. on 10 May 1958 (ABS reference collection). ABS is the southernmost locality where this species has been recorded

in Florida. Some populations of *S. calanus* in Florida are associated with oaks, whereas others occur on hickory. Oaks as well as Scrub Hickory (*Carya floridana* Sarg., Juglandaceae) are abundant at the station.

Strymon melinus melinus Hübner

STATUS: Abundant in Sand Pine scrub, sandhill, scrubby flatwoods, and disturbed sites.

HOST PLANTS: Observed ovipositing on *Desmodium incanum* flowers, and often associated with *Galactia* species.

FLOWERS VISITED: *Asclepias curtissii*, *Bidens alba*, *Dalea feayi*, *Diodia teres*, *Eriogonum floridanum* Small (Polygonaceae), *Eryngium cuneifolium*, *Galactia regularis*, *Lachnanthes carolinianum*, *Liatris tenuifolia*, *Licania michauxii* Prance (Chrysobalanaceae), *Palafoxia feayi*, *Sabal etonia*.

LYCAENIDAE: POLYOMMATINAE

Hemiargus ceraunus antibubastus Hübner

STATUS: Abundant in Sand Pine scrub and sandhill habitats.

HOST PLANTS: Observed ovipositing on *Cassia fascicularis*, *Indigofera hirsuta*, and *Galactia regularis* flowers. Larvae were found on *Chapmannia floridana* Torr. & Gray (Fabaceae) and *Indigofera carolinianum* flowers.

FLOWERS VISITED: *Asclepias curtissii*, *Balduina angustifolia*, *Dalea feayi*, *Diodia teres*, *Eriogonum floridanum*, *Eryngium cuneifolium*, *Lachnanthes carolinianum*, *Liatris tenuifolia*, *Licania michauxii*, *Satureja rigida*.

PARASITOID: *Rogas* species (Braconidae) reared from a larva on *Chapmannia*, 1 October 1986, T. Eisner (ABS reference collection).

Leptotes cassius theonus (Lucas)

STATUS: This species appears to colonize the station during favorable years. The reference collection has specimens from 1957 and 1960. I have not found the *Cassius* Blue at ABS, but several were seen in nearby Lake Placid during November 1987 in association with an exotic mimosoid tree. Frost (1964) supposedly collected a *Hemiargus thomasi bethunebakeri* Comstock & Huntington in a light trap at ABS; however, this species has been recorded only in the Florida Keys and southernmost mainland. Dr. Frank Fee kindly checked the Frost collection at Pennsylvania State University, examined the specimen, and determined that it is a female *L. cassius*, not *H. thomasi*.

NYMPHALIDAE: HELICONIINAE

Agraulis vanillae nigrrior Michener

STATUS: Occasional in scrubby flatwoods and disturbed sites, especially during the fall when dispersing adults fly southward through Florida in large numbers.

FLOWERS VISITED: *Bidens alba*, *Lachnanthes carolinianum*, *Liatris tenuifolia*, *Richardia scabra*.

Heliconius charitonius tuckeri Comstock & Brown

STATUS: Abundant during the fall in shady areas on the main grounds.

HOST PLANTS: Larvae were found on an exotic species of *Passiflora* (Passifloraceae) growing in the old citrus grove on Red Hill.

NYMPHALIDAE: NYMPHALINAE

Anartia jatrophae guantanamo Munroe

STATUS: Occasional to abundant during the fall, when adults of this tropical species disperse northward.

FLOWERS VISITED: *Lachnanthes caroliniana*, *Lippia nodiflora*, *Vernonia gigantea*.

Basilarchia archippus floridensis (Strecker)

STATUS: Uncommon and local around patches of willow near Lake Annie; observed once on the main grounds.

HOST PLANT: Larvae were found on *Salix caroliniana* Michx. (Salicaceae).

Euptoieta claudia (Cramer)

STATUS: I observed one adult at Hicoria on 27 November 1983. The Variegated Fritillary probably colonizes ABS in some years.

Junonia coenia (Hübner)

STATUS: Abundant in scrubby flatwoods and other habitats.

HOST PLANTS: Larvae were found on *Seymeria pectinata* Pursh (Scrophulariaceae).

FLOWERS VISITED: *Dalea feayi*, *Lachnanthes carolinianum*, *Liatris tenuifolia*, *Lyonia ferruginea* (Walt.) Nutt. (Ericaceae), *Satureja rigida*.

Marpesia petreus (Cramer)

STATUS: The Ruddy Dagger Wing rarely strays into Highlands County from tropical South Florida. Comstock and Comstock (1902) collected one in May at Avon Park. Frost took one at ABS on 16 December 1959 (Kimball 1965).

Phyciodes phaon (Edwards)

STATUS: Uncommon along roadsides and on Red Hill.

FLOWERS VISITED: *Bidens alba*.

Phyciodes tharos tharos (Drury)

STATUS: R. W. Pease Jr. took one on 19 December 1957 (ABS reference collection). I have not found the Pearl Crescent at ABS, although the larval food plants, *Aster* spp. (Asteraceae), are present. This butterfly is abundant and widespread throughout Florida. Its scarcity at ABS is a mystery.

Polygonia interrogationis (Fabricius)

STATUS: One specimen (form *fabricii*) was taken at ABS on 5 December 1965 (ABS reference collection). The Question Mark is abundant 40 km north of the station at Highlands Hammock State Park (H. D. Baggett pers. comm.).

Vanessa atalanta rubria (Fruhstorfer)

STATUS: Uncommon in the citrus grove on Red Hill and on the main grounds. Frost (1966) took one in an ultraviolet light trap.

HOST PLANTS: Larvae were found on *Boehmeria cylindrica* (L.) Sw. (Urticaceae).

FLOWERS VISITED: *Polygonella robusta*.

Vanessa virginiensis (Drury)

STATUS: Uncommon in the old citrus grove on Red Hill and in scrubby flatwoods.
FLOWERS VISITED: *Lachnanthes carolinianum* and *Lantana camara*.

NYMPHALIDAE: SATYRINAE

Hermeuptychia sosybius (Fabricius)

STATUS: Abundant in shady areas on the main grounds. Frost (1964) captured one in an ultraviolet light trap.
FLOWERS VISITED: *Bidens alba*.

Neonympha areolata areolata (J. E. Smith)

STATUS: Comstock and Comstock (1902) reported the Georgia Satyr to be "very common over marshes in April and May, both at Avon Park and Lake Josephine." At ABS, R. W. Pease Jr. collected a few in August and October 1960 (reference collection) and Oosting and Harvey (1976) recorded it in April 1975. I did not find *N. areolata* on my surveys of the station.

NYMPHALIDAE: DANAINAE

Danaus gilippus berenice (Cramer)

STATUS: Occasional in scrubby flatwoods and sandhill habitats. Brower's (1961, 1962) data suggest that *D. gilippus berenice* is more abundant than *D. plexippus* in Highlands County, especially during the summer.

HOST PLANTS: M. F. Minno found larvae on *Asclepias curtissii*, *Asclepias tomentosa* Ell. (Asclepiadaceae), and *Asclepias tuberosa* ssp. *rolfsii*. Brower (1961) also reports immatures on *Asclepias humistrata* Walt. and *Asclepias curassavica* L. (Asclepiadaceae) in Highlands County.

FLOWERS VISITED: *Bidens alba*, *Balduina angustifolia*, *Dalea feayi*, *Heterotheca subaxillaris*, *Lachnanthes caroliniana*, *Lantana camara*, *Liatris tenuifolia*.

Danaus plexippus plexippus (Linnaeus)

STATUS: Most abundant during spring and fall in disturbed scrub habitats, but also present and breeding in small numbers during the summer.

HOST PLANTS: Brower (1961) reports Monarch immatures on *Asclepias humistrata*, *Asclepias tuberosa* ssp. *rolfsii*, and *Asclepias curassavica* in Highlands County.

FLOWERS VISITED: *Bidens alba*, *Polygonella robusta*.

Faunal Composition

Seventy species of butterflies have been found at ABS. Eleven additional species have been recorded from Highlands County, but not Archbold (Table 1). The least-probable of these to be found at the station is *I. henrici margaretae* dos Passos, which seems to be a poor disperser and usually occurs in swamps with an abundance of *Ilex cassine* L. (Aquifoliaceae), a larval food plant. *Calephelis virginienis* (Guérin-Ménéville) is likely to be an overlooked resident at ABS. This metalmark occurs in flatwoods at Sebring (35 km north of ABS on the Lake Wales Ridge) similar to those present at the station. The other

TABLE 1. Butterflies recorded from Highlands County, Florida, but not the Archbold Biological Station.

Family	Species
Hesperiidae	<i>Calpodus ethlius</i> (Stoll) <i>Euphyes pilatka pilatka</i> (Edwards) <i>Poanes aaroni howardi</i> (Skinner) <i>Problemia byssus</i> (Edwards)
Pieridae	<i>Pieris rapae</i> (Linnaeus)
Lycaenidae	<i>Incisalia henrici margaretae</i> dos Passos
Riodinidae	<i>Calephelis virginiensis</i> (Guérin-Ménéville)
Nymphalidae	<i>Asterocampa celtis reinthali</i> Friedlander <i>Asterocampa clyton flora</i> (Edwards) <i>Danaus eresimus tethys</i> Forbes <i>Megisto cymela viola</i> (Maynard)

butterflies may eventually be recorded from ABS as stray individuals or temporary colonizers.

The butterfly fauna of the station is an ever-changing mixture of species. In any particular year, additional species may become established and others may disappear. Many butterflies are highly vagile and disperse great distances, which may account for the several species recorded from ABS as single individuals. Some species are dependent upon ephemeral weedy habitats or specific stages in fire-maintained communities, and must frequently colonize new areas. Changes in habitat and climate are likely to cause changes in the butterfly fauna. Highlands County is a rapidly changing area, and many natural areas are being converted to pastures, orange groves, and urban environments

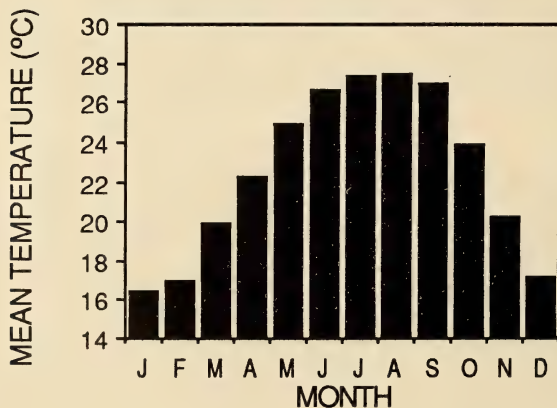


FIG. 3. Long-term mean monthly temperature at the Archbold Biological Station, Highlands County, Florida (National Oceanic & Atmospheric Administration 1987).

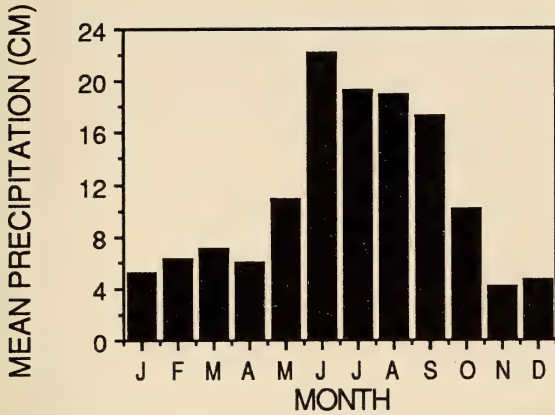


FIG. 4. Long-term mean monthly precipitation at the Archbold Biological Station, Highlands County, Florida (National Oceanic & Atmospheric Administration 1987).

(Peroni & Abrahamson 1985). ABS is changing in a different way. Large portions of the sandhill areas have not been burned for some time, and although small fires occur regularly in the flatwoods, large fires do not. Many areas of the station today look quite different from photographs taken in the 1930's (ABS archives).

A number of tropical species, including *Urbanus dorantes*, *Pyrgus oileus*, *Battus polydamas*, *Ascia monuste*, *Nathalis iole*, *Phoebis philea*, *Phoebis agarithe*, *Leptotes cassius*, *Heliconius charitonius*, and *Anartia jatrophae*, have a tendency to disperse northward, especially in the fall. These species occur sporadically at ABS. Some are known from single

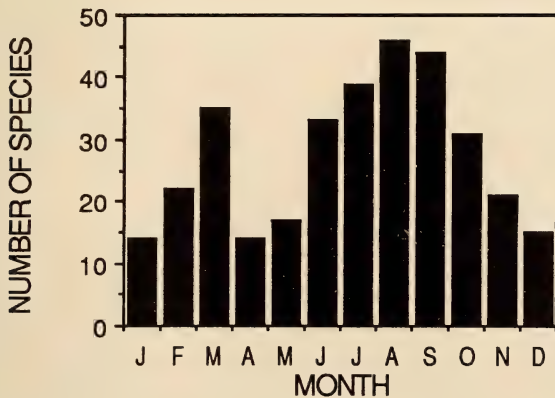


FIG. 5. The number of butterfly species recorded each month at the Archbold Biological Station, Highlands County, Florida.

TABLE 2. Records of monthly occurrence (indicated by an "x") of adult butterflies at the Archbold Biological Station, Highlands County, Florida.

Species	Month											
	J	F	M	A	M	J	J	A	S	O	N	D
Hesperiidae: Pyrginae												
<i>Epargyreus c. clarus</i>	—	—	x	—	—	—	x	x	—	—	—	—
<i>Erynnis brizo somnus</i>	x	x	x	x	—	—	—	—	—	—	—	—
<i>Erynnis horatius</i>	x	x	x	x	x	x	x	x	x	—	—	—
<i>Erynnis j. juvenalis</i>	x	x	x	—	—	—	x	—	—	—	—	—
<i>Erynnis z. zarucco</i>	—	x	x	—	x	x	x	x	x	x	—	—
<i>Pyrgus o. oileus</i>	—	—	—	—	—	—	x	x	x	x	x	x
<i>Thorybes pylades</i>	—	—	x	—	—	—	x	x	x	—	—	—
<i>Urbanus d. dorantes</i>	—	x	—	—	—	—	x	x	x	—	x	—
<i>Urbanus p. proteus</i>	x	—	x	—	x	—	x	x	x	x	x	x
Hesperiidae: Hesperinae												
<i>Ancyloxypha numitor</i>	—	—	—	—	—	—	—	x	—	—	x	x
<i>Asbolis capucinus</i>	—	—	—	—	—	—	—	—	x	—	x	—
<i>Atalopedes campestris huron</i>	x	x	x	—	—	x	x	x	x	—	—	—
<i>Atrytone d. delaware</i>	—	—	x	—	—	x	x	x	—	—	—	—
<i>Atrytonopsis hianna loammi</i>	—	—	—	—	—	—	—	—	x	—	—	—
<i>Copaeodes minimus</i>	—	—	—	—	—	x	x	x	x	—	—	—
<i>Euphyes arpa</i>	—	—	—	—	—	—	x	x	x	x	—	—
<i>Hesperia meskei straton</i>	—	—	—	—	—	—	—	—	—	x	—	—
<i>Hylephila p. phyleus</i>	—	x	x	—	—	—	x	x	x	—	—	—
<i>Lerema a. accius</i>	x	x	—	—	—	—	—	—	x	—	x	x
<i>Lerodea eufala</i>	—	—	—	—	—	—	—	x	x	x	—	—
<i>Nastra lherminier</i>	—	—	—	—	—	—	x	x	x	x	—	—
<i>Oligoria maculata</i>	—	—	x	—	—	x	x	—	x	x	—	—
<i>Panoquina o. ocola</i>	x	—	—	—	—	—	x	x	x	x	x	—
<i>Polites themistocles</i>	—	—	x	—	—	x	—	x	x	—	—	—
<i>Polites v. vibex</i>	—	x	x	x	—	x	x	x	x	—	x	—
<i>Wallengrenia otho</i>	—	—	—	—	—	x	x	x	x	x	—	—
Hesperiidae: Megathyminae												
<i>Megathymus yuccae buchholzi</i>	—	x	x	x	—	—	—	—	—	—	—	—
Papilionidae: Papilioninae												
<i>Battus p. philenor</i>	—	—	x	—	—	—	x	x	—	—	—	—
<i>Battus polydamas lucayus</i>	x	x	—	x	x	x	—	x	x	x	x	—
<i>Eurytides m. floridensis</i>	—	—	x	x	—	x	x	x	x	x	—	—
<i>Papilio cresphontes</i>	—	x	x	x	—	x	x	—	x	x	x	—
<i>Papilio glaucus australis</i>	—	—	x	x	x	x	x	x	x	x	—	—
<i>Papilio palamedes</i>	—	x	x	x	—	x	x	—	x	x	x	—
<i>Papilio polyxenes asterius</i>	—	—	x	x	x	x	—	—	x	x	—	—
<i>Papilio troilus ilioneus</i>	—	—	x	x	x	x	x	x	x	—	—	—
Pieridae: Pierinae												
<i>Ascia monuste phileta</i>	—	—	—	—	—	x	x	x	—	x	—	—
<i>Pontia protodice</i>	—	—	—	—	x	x	x	—	—	—	—	—
Pieridae: Coliadinae												
<i>Colias eurytheme</i>	—	—	—	—	x	x	—	x	x	—	—	—
<i>Eurema daira daira</i>	x	x	x	—	—	x	x	x	x	x	x	x
<i>Eurema l. lisa</i>	—	x	x	—	—	x	x	x	x	—	x	x
<i>Eurema nicippe</i>	x	—	—	—	—	—	—	x	x	—	x	—

TABLE 2. Continued.

Species	Month											
	J	F	M	A	M	J	J	A	S	O	N	D
<i>Nathalis iole</i>	—	x	x	—	—	—	x	—	—	—	—	x
<i>Phoebis agartithe maxima</i>	—	—	—	—	—	—	x	—	—	—	—	—
<i>Phoebis p. philea</i>	—	—	—	—	—	—	—	x	—	—	—	—
<i>Phoebis sennae eubule</i>	x	x	x	—	—	x	x	x	x	x	x	—
<i>Zerene cesonia</i>	—	—	x	—	x	—	—	x	—	x	—	—
Lycaenidae: Eumaeinae												
<i>Atlides h. halesus</i>	—	x	x	—	x	—	—	—	—	—	—	—
<i>Calycopis cecrops</i>	—	x	—	—	x	x	x	x	x	x	x	—
<i>Euristrymon favonius</i>	—	—	—	x	x	x	—	—	—	—	—	—
<i>Parrhasius m-album</i>	—	x	—	x	—	x	x	x	—	x	—	—
<i>Satyrrium c. calanus</i>	—	—	—	—	x	—	—	—	—	—	—	—
<i>Strymon m. melinus</i>	—	—	x	—	x	x	x	x	x	x	x	—
Lycaenidae: Polyommatainae												
<i>Hemiargus c. antibubastus</i>	—	—	x	—	—	x	—	x	x	x	x	x
<i>Leptotes cassius theonius</i>	—	—	—	—	—	—	—	x	—	x	—	x
Nymphalidae: Heliconiinae												
<i>Agraulis vanillae nigrior</i>	—	—	x	—	—	—	—	x	x	x	x	—
<i>Heliconius charitonius tuckeri</i>	—	—	—	—	—	x	—	x	x	x	x	—
Nymphalidae: Nymphalinae												
<i>Anartia jatrophae guantanamo</i>	—	—	—	—	—	—	—	x	x	x	—	—
<i>Basilarchia a. floridensis</i>	—	—	—	—	—	x	—	x	x	—	x	—
<i>Euptoietia claudia</i>	—	—	—	—	—	—	—	—	—	—	x	—
<i>Junonia coenia</i>	—	—	x	—	—	—	x	x	x	x	x	—
<i>Marpesia petreus</i>	—	—	—	—	—	—	—	—	—	—	—	x
<i>Phyciodes phaon</i>	—	—	x	—	—	x	—	—	x	—	—	—
<i>Phyciodes t. tharòs</i>	—	—	—	—	—	—	—	—	—	—	—	x
<i>Polygonia interrogationis</i>	—	—	—	—	—	—	—	—	—	—	—	x
<i>Vanessa atalanta rubria</i>	x	x	—	—	—	x	x	—	—	—	—	x
<i>Vanessa virginienis</i>	—	—	x	—	—	—	x	—	—	—	—	—
Nymphalidae: Satyrinae												
<i>Hermeuptychia sosybius</i>	x	x	x	—	x	x	—	—	x	x	x	x
<i>Neonympha a. areolata</i>	—	—	—	x	—	—	—	x	—	x	—	—
Nymphalidae: Danainae												
<i>Danaus gilippus berenice</i>	—	—	x	—	x	x	x	x	x	—	x	x
<i>Danaus p. plexippus</i>	—	—	x	x	x	x	x	x	—	x	—	x

individuals; others establish ephemeral populations during favorable years. A few butterflies migrate southward through Florida in great numbers during the fall (Walker 1978, 1985). Southward-bound migrants such as *Urbanus proteus*, *Panoquina ocola*, *Eurema daira*, *Phoebis sennae*, *Agraulis vanillae*, and *Junonia coenia* occur in greatest abundance at ABS during late August, September, and October.

There are no butterflies endemic to the scrubs of the Lake Wales Ridge (Deyrup 1989), but several are found primarily in peninsular

Florida. Peninsular Florida endemics that occur in Highlands County include *Erynnis brizo somnus*, *Euphyes arpa*, *Papilio glaucus australis*, *Papilio troilus ilioneus*, *Eurytides marcellus floridensis*, *Satyrium calanus calanus*, *Incisalia henrici margaretae*, *Euristrymon favonius*, *Basilarchia archippus floridensis*, *Asterocampa celtis reinthali*, and *Asterocampa clyton flora*. None of these butterflies are rare or endangered.

Phenology

Figures 3 and 4 show climatological data for ABS. The wet season corresponds to summer, beginning in May and ending in October. Temperature (Fig. 3) and rainfall (Fig. 4) peak between June and September. Although adult butterflies may be found all in months at the station, there are two peaks in species richness and abundance (Fig. 5). The first peak occurs in March, when species overwintering as immatures break diapause, complete development, and emerge as adults. A second peak occurs in late summer and early fall (August/September), when most resident species reach their greatest abundance and many migrant butterflies travel through Highlands County. Table 2 presents the monthly occurrence of each species at ABS.

The majority of butterfly species at ABS are multivoltine, but some species, particularly oak-feeders, emerge as adults only in the spring or early summer. Univoltine species include *Erynnis brizo*, *Erynnis juvenalis*, *Megathymus yuccae*, *Satyrium calanus*, and *Euristrymon favonius*. Spring adults of multiple-brooded species often are smaller or patterned somewhat differently from later generations. This is especially true of those that overwinter in the pupal stage, such as swallowtails (Papilionidae). A few butterflies found at ABS overwinter in the adult stage. Adult diapausing species often have different summer and winter phenotypes, as in *Pyrgus oileus*, *Eurema* spp., *Zerene cesonia*, *Junonia coenia*, *Phyciodes phaon*, and *Phyciodes tharos*. The winter forms of most of these species are brownish or reddish on the undersides of the hindwings, instead of the paler colors of summer individuals.

Adult and Larval Resources

At least 70 of the approximately 620 species of vascular plants that grow at ABS are used by butterflies as larval hosts or as sources of nectar for adults. Only about 13% of the flora consists of monocots; yet the larvae of nearly 30% of the butterfly species feed on plants in this group, such as grasses, sedges, palms, and yuccas. Among the dicots, the Asteraceae, Fabaceae, Fagaceae, Lamiaceae, Rubiaceae, and Verbenaceae are the more important families used by butterflies.

A few rare plants such as *Asclepias curtissii*, *Conradina canescens*, *Eryngium cuneifolium*, and *Liatris ohlingerae* are used occasionally by butterflies at ABS. On the other hand, exotics like *Aristolochia literalis*, *Citrus* spp., *Clerodendrum speciosissimum*, and *Wedelia trilobata* are used as well. The flowers of weedy plants such as *Bidens alba* and *Lantana camara* may be visited by multitudes of butterflies during late summer and fall, but are often ignored at other seasons. Native plants with flowers attractive to many butterflies include palmettos, *Asclepias* spp., *Lachnanthes carolinianum*, *Dalea feayi*, *Balduina angustifolia*, *Liatris* spp., and *Satureja rigida*.

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GENERAL NOTES

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OCCURRENCE OF *DISPHRAGIS CAPTIOSA* (NOTODONTIDAE) IN ARIZONA

Additional key words: Mexico, national record, United States.

There have been specimens of a notodontid from Arizona in the Natural History Museum of Los Angeles County (LACM) for over 40 years. The species was identified as *Disphragis captiosa* Draudt, 1932, but the identification was made too late for its inclusion in McDunnough's 1938 Checklist. The record remained unpublished, and subsequently was left out of the 1983 MONA Checklist (Franclemont 1983). This note will facilitate its inclusion in a subsequent list.

Disphragis captiosa was described by Draudt (1932) from specimens collected in Zacualpan and Cuernavaca, Mexico. The type is a female in the Draudt collection. The female is similar to the female of *Heterocampa obliqua* Pack., 1864, in general appearance, but much smaller (33 mm versus 47 mm). Specimens were taken in Madera Canyon, Santa Cruz Co., Arizona, on 22 and 25 August 1946, and 17 and 20 August 1949 by J. A. Comstock, L. M. Martin, and C. W. Kirkwood (LACM). I collected a single specimen in a residential area on the north side of Tucson, Pima Co., Arizona, on 11 August 1974. The LACM also has one specimen from Rincon, Puntarenas Province, Costa Rica, which may represent the southern extent of its range.

All six specimens examined are females as is the type. I hope that this note will stimulate Arizona collectors to generate more records for this species, and perhaps collect the male. *Disphragis captiosa* can be recognized by a large oval yellow-brown patch on the forewing, that starts at the reniform and extends outward toward the apex and outer margin.

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HILEITHIA DECOSTALIS (CRAMBIDAE: PYRAUSTINAE), NEW TO THE UNITED STATES

Additional key words: distribution, new record, checklist placement.

Hileithia decostalis (Guenée, 1854) is a relatively small pyraustine moth native to the neotropics. Although there is a specimen from Mexico in the collection of the USNM (A.

Solis, pers. comm.), it formerly was not known to occur as far north as the United States (Munroe 1983). A single female was taken at Bay St. Louis, Hancock Co., Mississippi, 30 July 1979, by Rick Kergosien. The specimen was determined by E. Munroe and is deposited in the personal collection of B. Mather. *Hiliethia decostalis* should be inserted in the checklist (Munroe 1983) as number 5271.1, preceding *Herpetogramma* Lederer.

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A NEW LICHEN MOTH RECORD FOR THE UNITED STATES: *LYCOMORPHODES SORDIDA* (ARCTIIDAE: LITHOSIINAE) FROM SOUTH TEXAS

Additional key words: Zygaenidae, mimicry, neotropical, Hidalgo County.

Lycomorphodes sordida (Butler) (Arctiidae: Lithosiinae) is distributed in Latin America from northern Mexico to northern Colombia (Seitz 1940:253). The species is sexually dimorphic; both sexes are presumably lycid beetle (Lycidae) mimics. The male has nearly solid orange forewings, with the wing margins variably shaded with black. The female forewing is similar, but has a black costal dash midway between the base and apex, and the margins are more heavily shaded with black. The hindwing of both sexes is generally black, with only the leading edge suffused with orange. *L. sordida* is a small species; male forewing length ranges between 18 and 20 mm ($n = 9$); females range between 21 and 23 mm ($n = 7$). Superficially, *L. sordida* resembles some species of Zygaenidae (e.g., *Triprocris* spp.), which also are probable lycid beetle mimics, though the zygaenids tend to have less heavily scaled wings giving them a translucent appearance.

Lycomorphodes sordida may be locally common in northern Mexico. I have found it especially abundant in Tamazunchale in the state of San Luis Potosí (at mercury vapor street lights in August). I recently examined a male specimen of *L. sordida* in the personal collection of J. Richard Heitzman with the following data: Santa Ana Reserve, Hidalgo County, Texas, 24 June 1968, taken at UV light, J. R. Heitzman. [The full title of the Santa Ana Reserve is Santa Ana National Wildlife Refuge.] The specimen had been determined as "*Triprocris* sp.??". Species in the genus *Triprocris* are not likely to occur in southern Texas; the genus is generally restricted to the southwestern U.S. and northwestern Mexico (Seitz 1940: 24–25). The range of *L. sordida* is unlikely to overlap broadly with that of any *Triprocris* sp. This U.S. record of *L. sordida* probably has gone unnoticed due to the small size of the species and the previous misdetermination.

The Check list of the Lepidoptera of America North of Mexico (Hodges et al. 1983: 114–115) does not list *Lycomorphodes sordida* as part of the fauna of North America north of Mexico. The specimen discussed above was sent to Douglas Ferguson at the U.S. National Museum of Natural History (where the specimen now resides) to confirm my identification and to verify that this is indeed the first U.S. record for *L. sordida*. The specimen subsequently was examined by Nancy L. Jacobson, who also confirmed the identification.

The genus *Lycomorphodes* is distributed widely throughout Latin America. Of the ± 15 species in the genus, *L. sordida* is the most northerly in distribution, with the majority of the species occurring in South America (Seitz 1940: 252–254). Although there is some resemblance to the zygaenid genera *Tripocris* Grote and *Pyromorpha* Herrich-Schaeffer, confusion is more likely with the lithosiine genera *Lycomorpha* Harris and *Ptychoglene* Felder (also apparent lycid beetle comimics), some species of which are sympatric with *Lycomorphodes sordida* in northern Mexico. Specimens of lithosiine arctiids that have been collected in south Texas and determined as *Lycomorpha* or *Ptychoglene* sp. should be reexamined closely to determine if they represent additional U.S. records of *Lycomorphodes sordida*.

I thank J. R. Heitzman for allowing me to have and examine the male *L. sordida*, and Douglas Ferguson and Nancy L. Jacobson for verification of the identity of the specimen and critically reviewing the manuscript.

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LIFE HISTORY NOTES ON CATOCALA SAPPHO AND CATOCALA ULALUME (NOCTUIDAE)

Additional key words: larvae, rearing, foodplants, Lepidoptera.

I present new life history information for two Nearctic species of underwing moths, including a description of the larva of *Catocala sappho* Strecker, and a wild foodplant record for *Catocala ulalume* Strecker.

Catocala sappho. In Florida, adults of this underwing species can be found in ravine bottomland habitats between late May and early August. Adult males are collected most easily in mid to late afternoon as they rest on tree trunks about 1–3 m above the ground; females are encountered less frequently. The preferred microhabitat of the species seems to be low-lying hardwood hammocks that flood in the late winter and early spring, and whose characteristic trees include pignut hickory (*Carya glabra* [Mill] Sweet; Juglandaceae), bayberry (*Myrica cerifera* L.; Myricaceae), sweetgum (*Liquidambar styraciflua* L.; Hamamelidaceae), and several species of oaks (*Quercus* [Tourn.] L.; Fagaceae).

In July of 1986, three adult female *Catocala sappho* were collected from tree trunks in Gainesville, Alachua County, Florida, and a fourth was taken in a bait trap in Jacksonville, Duval County, Florida. Each female was put in a separate large paper bag and supplied with suitable food on a daily basis (sucrose solution placed on a small piece of sponge), and small twigs of hickory (the presumed foodplant; see below) to stimulate oviposition. The bags were misted with water every two days to prevent desiccation. One of the Gainesville females deposited approximately 50 eggs on 14–15 July 1986; the others died without ovipositing, although dissections revealed the presence of mature eggs in each. Eggs were deposited in clusters in the folds of the paper bag, on the sides of the bag, and on the sponge. The eggs subsequently were transferred to baby food containers with screened lids, which were stored outdoors in a shaded location through the winter.

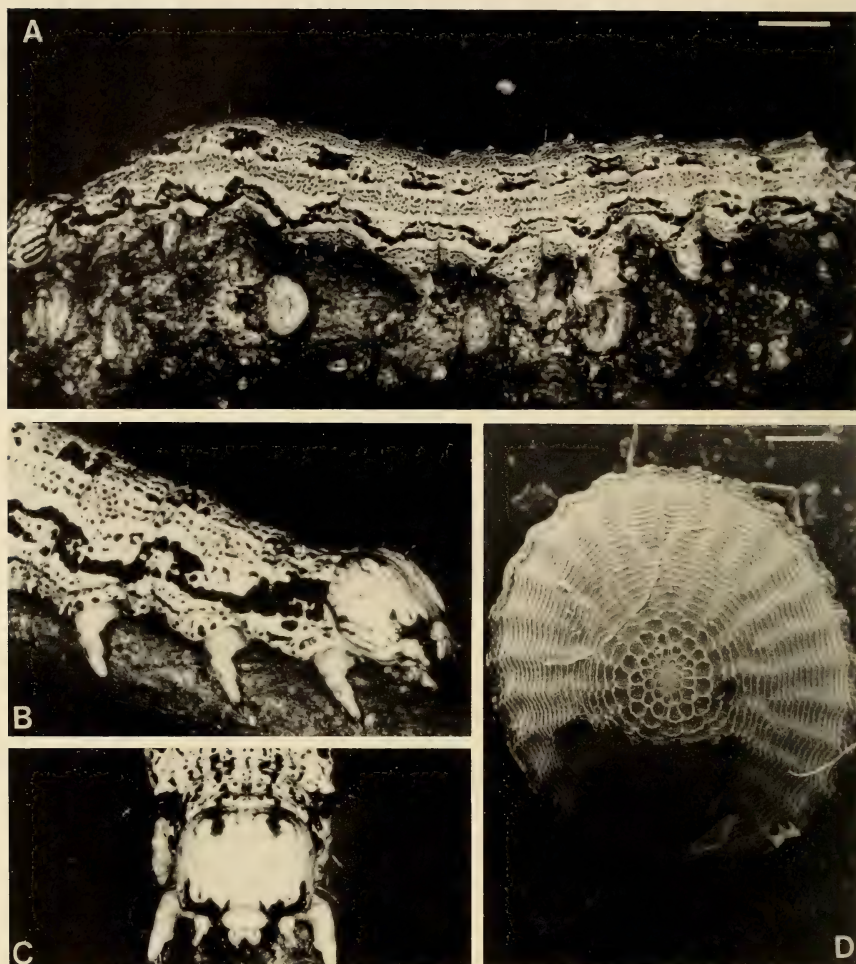


FIG. 1. A–C, mature (sixth instar) larva of *Catocala sappho* Strecker: A, lateral view, scale bar = 5 mm; B–C, enlargements of head capsule and prothoracic regions. D, scanning electron micrograph (SEM) of egg: at 80 \times magnification, scale bar = 0.2 mm; note larval exit hole at bottom.

The first larvae hatched on 22 March 1987. The remainder of the batch hatched within a few days. The young larvae were very active and readily accepted young leaves of pignut hickory, but refused mockernut hickory (*Carya tomentosa* [Poir.] Nutt.; Juglandaceae). Several larvae from the same brood in the care of L. F. Gall and W. A. Miller readily accepted shagbark hickory (*Carya ovata* [Mill.] K. Koch; Juglandaceae) and pignut hickory, but fed sparingly on pecan (*Carya illinoensis* [Wang.] K. Koch; Juglandaceae). My rearing procedure was to place young larvae in small plastic containers with tight fitting lids, and to change leaves every other day. The more mature larvae were transferred to large screened plastic cages, with foodplant leaves "potted" in test tubes containing water. The mature larvae had a habit of dropping from the foodplant and thrashing and twisting when disturbed. Feeding at all stages of growth was usually at night, although

daytime feeding did occur. The larvae passed through six instars; the first pupated on 19 April 1987. The first adults hatched on 19 May 1987. The cocoons were typical for *Catocala*: loosely spun silk, incorporating paper towels and/or leaf litter at the bottom of the rearing containers.

The mature larva of *Catocala sappho* is shown in Figs. 1A–1C. The larval ground color is whitish gray, finely stippled with black atoms; some larvae are sparsely covered with a waxy white bloom; the dorsal tubercles are small and red, set inside whitish rings; the fifth abdominal segment is raised only slightly dorsally, and has an indistinct, mottled dark gray lateral “saddle patch;” the two dorsal stripes are black, prominent (especially on the mesothorax), but interrupted throughout their length; the latero-dorsal stripes are black, prominent, and less interrupted than the dorsal stripes; short, thin fleshy “filaments” are scattered sparingly along the latero-ventral margins; the venter is whitish, with indistinct pinkish spots rimmed with gray on the abdominal segments; the head capsule is whitish gray, with fine pinkish-red and black striations, with neither a lateral band nor conspicuous submandibular dash.

Pecan (*Carya illinoensis*) is listed, without supporting evidence, as a larval foodplant for *Catocala sappho* by Forbes (1954), Kimball (1965), and Sargent (1976). Kimball additionally listed “hickory” as a foodplant for *Catocala sappho*, and cited Watson (1919), although Watson stated only that: “Its life history is entirely unknown. Its relatives spend their caterpillar days on the hickory and it is probable that this one does likewise. It is found only in woods with hickories.” On the basis of (1) my experience with the habitat of adult *Catocala sappho*, which agrees with Watson’s observations, (2) the rearing notes presented herein and by Gall (1992), and (3) the overall geographic range of the moth, it seems unlikely that pecan is a wild host of any significance (being either recorded in error, given that misidentifications of hickories are common; or in confusion with *ex ovis* foodplant acceptability). Hickories in section §*Eucarya* DC. of *Carya* (e.g., *Carya glabra*) seem much more probable candidates.

Catocala ulalume. On 26 May 1986, I collected a full grown larva of what subsequently proved to be *Catocala ulalume* on a small mockernut hickory (*Carya tomentosa*) in Liberty County, Florida. The habitat in which the larva was found was dominated by scrubby oak, with a mixture of mockernut hickories and species of hawthorn and blueberries. The larva pupated on 31 May 1986, and an adult female emerged 29 June 1986. I am not aware of any previously published wild foodplant records for *C. ulalume*. Brower (1922) provided a description of the larva based on *ex ovis* rearings.

I thank H. D. Baggett and R. M. Gillmore for stimulating my interest in *Catocala*, and for sharing their considerable knowledge about these moths in Florida. L. F. Gall helped edit the manuscript and hunt down references.

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BOOK REVIEWS

BUGGY BOOKS: A GUIDE TO JUVENILE AND POPULAR BOOKS ON INSECTS AND THEIR RELATIVES, by Gary A. Dunn. 1990. Published by Young Entomologists' Society, Inc., 1915 Peggy Place, Lansing, Michigan 48910-2553. 120 pp. Soft cover, 21 × 28 cm, no ISBN, \$12.95 (plus \$2 S&H).

Asked by a clergyman what his many years of studying biology had taught him about the Creator, the great scientist J. B. S. Haldane reportedly replied "An inordinate fondness for beetles." Apocryphal or not, this anecdote underscores the fact that the insect order Coleoptera is the most species-rich group of animals on earth, currently numbering about 350,000 named species. Extending Haldane's logic, we must surmise that the Creator prefers beetles over butterflies and moths by a three-to-one margin; the Order Lepidoptera numbers about 120,000 named species, barely edging out Diptera (flies) for a distant second place. Hymenoptera (ants, bees, and wasps) comes in fourth at about 100,000 species before the insects relinquish fifth place to the Mollusca (a Phylum, no less) at around 80,000 species. Order Hemiptera (true bugs) ranks sixth at 60,000 species, followed by spiders (Class Arachnida—55,000 spp.), vertebrates (Phylum Vertebrata—54,000 spp.), and crustaceans (another Class—45,000 spp.), before we arrive at the Order Orthoptera (grasshoppers, crickets, roaches) in tenth place with 20,000 species. (These numbers are taken from Southwood, T. R. E., 1978, *The components of diversity*, pp. 19–40, in Mound, L. A. & N. Waloff (eds.), *Diversity of Insect Faunas*, Symposia of the Royal Entomol. Soc. London, No. 9; Blackwell Sci. Pub., Oxford, 204 pp.)

These numbers and rankings are useful in evaluating the attention given different groups in popular publications on insects. Does popularity have anything to do with diversity? Assessing the relative popularity of insect orders in books for the general public recently has been made easier by Gary Dunn, who has compiled a list of 736 juvenile and popular books on insects and their relatives. *Buggy Books* covers only non-fiction works (fictional books on arthropods number an additional several hundred titles and will be covered in a future publication), but stretches back to 1900 to cover 90 years of publishing.

The heart of *Buggy Books* is an alphabetical listing by title in two parts. Part 1 treats non-insect arthropods; Part 2 treats insects. In each Part, following the alphabetical book list, is a subject index, age appropriate index, and an author index. For each book entry the following information is given: author; name, place, and date of publication; number of pages and illustrations; ISBN; price at the time of publication; an age appropriateness abbreviation; a quality rating symbol; and a brief description (2–3 lines). Age appropriateness designations are based on publisher recommendations and Dunn's own evaluations. Intended as guidelines, not absolutes, the five age categories range from PRE/BEG (=Read-aloud and Early Reader Books, ages 3–6) to INT/ADV (=Books for Adolescents and Adults). The quality ratings are Dunn's personal opinion of the quality and usefulness of the book. They range from one star (Books of POOR Quality = little use) to five stars (Books of EXCELLENT Quality = highly useful). A significant minority of titles were unavailable for review and are labeled NR (=not rated).

The indices add greatly to the usefulness of *Buggy Books*. For example, in the Age Appropriateness Index, titles are grouped alphabetically under each of the five categories and are followed by the quality rating, providing easy identification of the best books appropriate for children of classrooms of any age group. In the Subject Index, titles are listed alphabetically under subject headings (5 subject categories in Part 1; 24 categories in Part 2), and each title is followed by the age appropriateness designation. My one suggestion for improvement of *Buggy Books* would be to add the quality ratings to titles listed by subject. This would allow someone interested in a particular group—butterflies and moths, for example—to scan for the top quality books about those insects.

Dunn, Executive Director of Y.E.S. (Young Entomologists' Society), has tried to make *Buggy Books* as complete as possible, but admits that it is unlikely that he has uncovered every non-fiction arthropod book ever published in English (books published in other languages have not been included). Even so, nothing else approaches the comprehen-

siveness of this compendium. For parents and teachers, *Buggy Books* is an invaluable resource for locating quality books (and avoiding inferior ones) that will stimulate young naturalists and introduce them to the animal groups that display the greatest diversity in species, life histories, and behavior. To be sure, many titles are out-of-print, but "collecting" these rarities can be as challenging and exciting for the bibliophile as swinging a net is for the field lepidopterist. Many in-print titles are available by mail from Y.E.S.'s Buggy Bookstore, or by special order from any good bookshop. To locate out-of-print titles, Dunn suggests checking your local public or school library (ask for a search through interlibrary loan if the book is unavailable locally) or exploring used bookstores.

Let's return to our original question: Does popularity (number of titles) have anything to do with diversity (number of species)? Here's the score for the Orders of insects:

Order	(Rank)	Percentage of species in Class Insecta	Number of books published on Order since 1900	Percentage of total books published	(Rank)
Coleoptera	(1)	44.2%	39	10.8%	(3)
Lepidoptera	(2)	15.1%	137	37.9%	(1)
Diptera	(3)	15.0%	13	3.6%	(6)
Hymenoptera	(4)	12.6%	113	31.3%	(2)
Hemiptera	(5)	7.6%	6	1.7%	(7)
Orthoptera	(7)	2.5%	38	10.5%	(4)
Other Orders	(6)	3.0%	15	4.2%	(5)
Totals		100.0%	361	100.0%	

The great popularity of the Lepidoptera probably results more from public appreciation of the beauty and grace of butterflies than from the sheer number of species, most of which are small dull-colored moths. Indeed, most of the books treat butterflies, which account for only about 15% of the Lepidoptera. No doubt the mystical symbolism of metamorphosis contributes as well, as many books dwell on the "magic" and "wonder" of the transformation from caterpillar to adult. (Of course, the four most species-rich orders are all holometabolous, but the immature stages of beetles, flies, and hymenopterans are usually much more cryptic than woolly bears, horned devils, and cutworms.) Hymenoptera surely owes its boost in the rankings in part to its venomous nature (killer bees and warrior ants are favorite book subjects) and perhaps to widespread envy of the industrious nature of ubiquitous ants. Flies would probably rank higher if they weren't generally perceived as pests and carriers of disease. That domestic species tend to breed in disgusting places doesn't help.

I could go on, but in keeping with the spirit of self-discovery encouraged by *Buggy Books*, I'll let you ponder the numbers and draw your own conclusions.

BOYCE A. DRUMMOND, *Natural Perspectives*, P.O. Box 9061, Woodland Park, Colorado 80866.

DIE RAUPEN DER SCHMETTERLINGE EUROPAS, by Prof. Dr. Arnold Spuler (ZWEITE AUFLAGE VON DR. E. HOFMANN'S GLEICHNAMIGEM WERKE). Erlangen, Weihnachten 1904. Reprint edition 1989, Apollo Books, Svendborg, Denmark. In German. 38 pp. "introduction" and appendix; 60 color plates, 2000+ figures. Hard cover, 21 × 29 cm, ISBN 87-88757-12-9, Danish Kroner 780 (about \$125 U.S.).

The title indicates that this is a book about the caterpillars of European butterflies, but 6.5 plates are butterfly immatures, 42.5 plates are moth immatures, 1 plate is eggs, and 9.5 of the 10 addendum plates are moth larvae.

The book appears to be an exact reprint of the 1904 edition (but I have not compared it with the original). As a consequence, the text is vintage 1904, and has limited value (especially if one is not fluent in German). The "introduction" of 26 pages is the entire text and covers a diversity of topics, including a general review on insects, a similar, but more detailed review for Lepidoptera, including details on eggs, larvae and pupae, ranging from structure to biology, behavior, and life cycles. Useful and harmful larvae are listed, examples of natural enemies are given, diseases are discussed, and culturing techniques are described. Other techniques are also provided, including killing adults by chloroform, cyanide, tobacco juice or smoke, and how to anesthetize and inflate larvae. The eleven-page "appendix" contains indices to common names and scientific names of plants, and an index to the Lepidoptera species associated with them. The genera of the insects are not indexed, so, for example, one cannot easily look up which species of *Malacosoma* are covered. The extensive use of German common names is also a drawback unless one is very familiar with the language.

However, the book's primary value is in the beautiful color illustrations, not the text, and it is certainly more useful for Europeans than North Americans, unless one wants to gaze upon a cabbage butterfly larva or a gypsy moth larva and a few others. The plates are nicely laid out as is characteristic of many of the old Lepidoptera books, with the caterpillars resting on vegetation in more or less natural positions, and with many flowers included. I judge most of the larvae to be last instars, and, as a general rule, the larger and more distinctive the larva is, the easier it will be to identify it using the illustrations. However, the gypsy moth larva is rather poorly done, and it would be easy to overlook it in making comparisons. The smaller illustrations cannot show much detail, and the best they can do is give an overall impression of the color and of any patterns or distinctive structures that are readily apparent. The illustrations are generally grouped by families, but families are not given anywhere, making the book less useful to those who are not very knowledgeable. The nomenclature is obviously outdated, but can't be corrected in a strict reprint edition. The paper, printing, color reproduction, and binding appear to be excellent. I don't know what the original 1904 edition sells for on the used/rare book market, but the \$125 price of this reprint will probably deter all except those who are lovers of old color plates (and a reprint is not quite the same as an original).

In summary, the book is a nice reproduction of an old caterpillar plate book that some may find enjoyable and useful.

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A REVISION OF THE INDO-AUSTRALIAN GENUS *ATTACUS*, by Richard S. Peigler. 1989. Lepidoptera Research Foundation, 9620 Heather Road, Beverly Hills, California 90210. xi + 167 pp., 24 text figs., 4 color plates. Soft cover, 20 × 28 cm, ISBN 9611464-2-7, \$30.00.

Peigler has done an outstanding piece of work in revising the "well known" moths of the genus *Attacus*. The members are among the largest of moths, and are arguably the

most widely recognized insects in the world. They occur from northern India and southern China to northern Australia. As a result of the interest in them, a considerable number of papers and descriptions have been published, usually without much prior knowledge of what was already in the literature. The result has been chaos. Now it is possible to go to one publication and learn to distinguish the 14 included species, to obtain the correct names for them, and to find out the status of all the other names that have been proposed. These total 50 (the emendations of which balloon the total to over 100!) for the species now included in *Attacus*. Plus anything and everything that pertains to these moths.

All of this is accomplished in a handsome, soft cover book, printed on glossy paper with wide margins; typographical errors are almost non-existent. The book is well organized and easy to use. In addition to the introduction, literature review, materials and methods, there are sections on morphology (egg, larva, pupa, and adult), systematics, biology and ecology, relationships of genera within the Attacini, zoogeography, phylogeny and speciation, and conclusions. There are over 10 pages of literature citations, an extremely valuable section of the book. The two appendices list recorded foodplants of *Attacus* and zoogeographical names, providing valuable help for an area in which so many name changes have taken place.

The illustrations are grouped in the back of the book. The black and white figures include distribution maps, morphology (larva, pupa, adult, venation), male and female genitalia, and cladograms. The four color plates show 3 caterpillars and 33 adults; the latter are reduced and of the right side only, due to the large size of these moths. The colors are quite good. All 14 species are shown, with type material of half of them being illustrated.

This is one of the best revisionary works on Lepidoptera to have been published; it sets a model for others to follow. I strongly recommend this revision to anyone who has any interest in these very large and showy moths, or in seeing a first-rate revisionary study. For me, it was well worth the cost of the book to have all the nomenclature cleared up, with just the species names themselves being utilized.

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A REVISION OF THE INDO-AUSTRALIAN GENUS *ATTACUS*, by Richard S. Peigler. 1989. Lepidoptera Research Foundation, 9620 Heather Road, Beverly Hills, California 90210. xi + 167 pp., 24 text figs., 4 color plates. Soft cover, 20 × 28 cm, ISBN-9611464-2-7, \$30.00.

Peigler revises this genus of tropical saturniine saturniid moths as thoroughly as is humanly possible with museum specimens and old literature. He then comes to us on bended knee and apologizes for doing this for a land he has never set foot in! As I read through this magnificent effort, I put on my "living in a developing tropical country hat" and asked "What would I have wanted Peigler to do with *Attacus*?" Would I have wanted him to spend years raising money to tourist around southeast Asia collecting an *Attacus* here and there, and soaking up the humidity and color of *Attacus* habitats? No.

Without doubt I would have wanted him to do exactly what he did. Peigler has taken one of the most conspicuous and tractable insects of southeast Asia, and cleaned the last two centuries of garbage and debris off the framework. As I turn page after page of Peigler's detailed and painstaking analysis of bad taxonomy, bad literature, printer's errors, bad biology, rare books, fractured journals, and bad specimens, and all the last century of taxonomic exploration by mediocre biologists and taxonomists in three European languages, I thank God for the Richard Peiglers of the world.

Can you imagine what hell it would have been for a Javanese biologist to have to spend four years of his life trying to sort out this mess before going to work on these fascinating

moths? What Peigler has done is swept all that muddled antiquariat into a snug and concise library file, sunk 38 names, and given us 14 taxonomically and nomenclatorially clean names. He has fulfilled the taxonomist's real mission. He has set up *Attacus* for a broad scale attack, by a southeast Asian resident, on its biology, ecology, natural history, ethology, morphology, cladistics, genetics, and chemistry. A clean taxonomy and nomenclature is the best start that any biologist can ask for in the tropics. If only we had a Peigler for every tropical genus with more than five species. And what a miracle it would be if all taxonomists had Peigler's ability and desire to elicit collaboration and help as he has done from the remainder of the community of workers on saturniid moths.

There may even be some more species of *Attacus* in southeast Asia, and now the resident biologist—anywhere between India and New Guinea—has a serious chance of finding them, knowing them, and using them.

And can you believe it? Peigler even had the common sense to put summaries in Bahasa Indonesia and Japanese at the beginning of his work. These are followed by a historical review of the taxa above *Attacus*, and a very detailed account of each of the 14 species. Not surprisingly, the two new species are known from only one and three specimens and are from small islands. Not only has Peigler cleaned up and summarized for the resident tropical biologist the old taxonomic literature on *Attacus* in developed world publications and museums, but he has done the same with the biological information on parasites, food plants, flight periods, and habitats occupied by *Attacus*.

Peigler finishes with a detailed analysis of the phylogenetic relationships between *Attacus* and the other genera of the tribe Attacini. He presents the logic and cladistic technology that lead to the postulation of a multi-branched phylogeny with *Attacus* and the eight other attacine genera, with the old world genera as one group and the new world genera as another. However, I cannot avoid noting that either *Rothschildia* and *Attacus* are one of the most incredible cases of convergence in color pattern available (which I doubt), or *Rothschildia* and *Attacus* represent the color pattern of the original saturniid species that gave us the Attacini. This in turn implies that the life form of these moths dates back at least to a time approximating the beginnings of continental separation. And even more tantalizing is his observation that the one *Enicospilus* ichneumonid wasp reared from *Attacus atlas* in West Malaysia is of the same *Enicospilus* species group that attacks *Rothschildia* and other large saturniine saturniids in the New World.

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OBITUARY

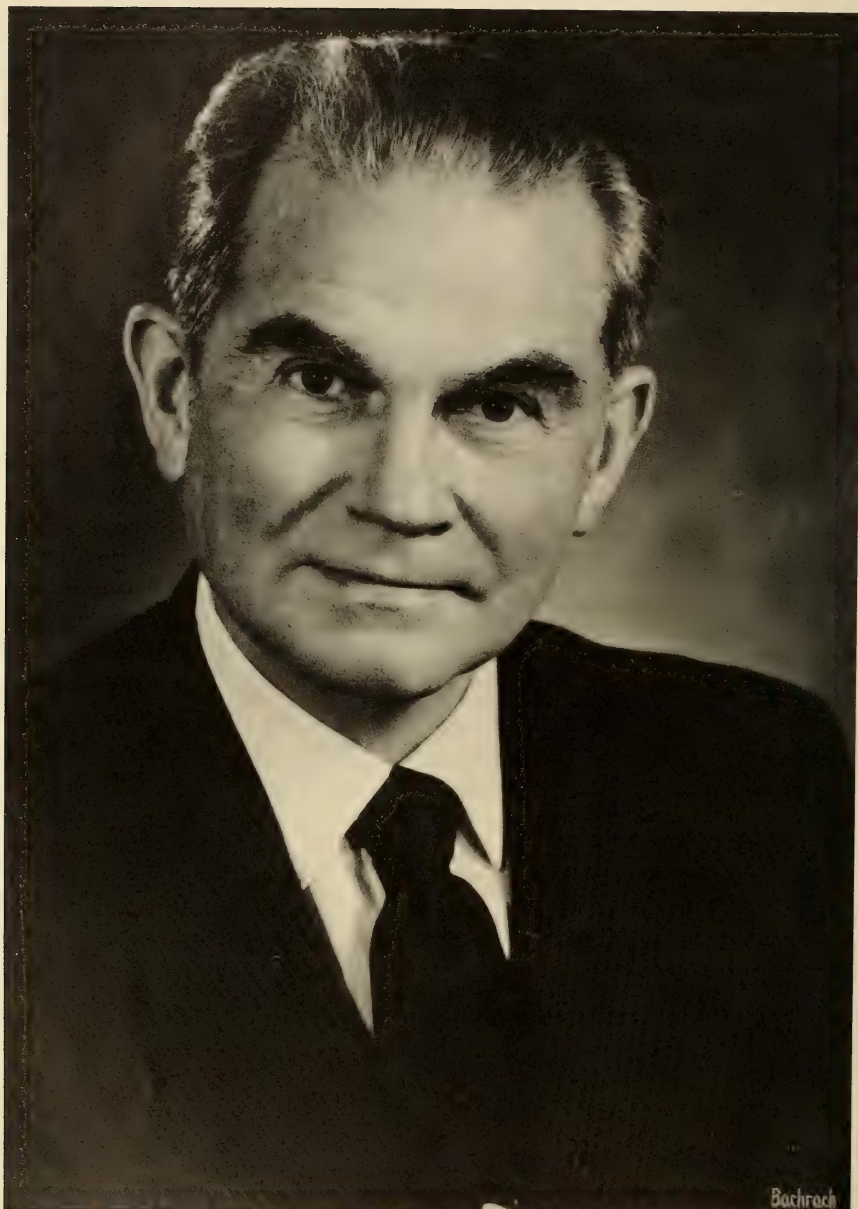
CARROLL MILTON WILLIAMS (1916-1991)

Carroll Williams, one of the country's most influential biologists, died in November 1991 after a long battle with a lymphoma. A dedicated lepidopterist in his youth, he graduated from the University of Richmond in 1937, and completed his formal training at Harvard University, where he earned both a Ph.D. in Zoology and a degree in medicine. He was appointed Assistant Professor of Zoology at Harvard in 1946, and remained on that faculty without interruption, serving as Chairman of Biology in 1959-62, and becoming the Benjamin Bussey Professor of Biology in 1966, until retiring in 1987. He is survived by his wife Muriel V. Williams, two sons, and a host of biologists whose careers he had helped to guide.

He followed closely the new biology that unfolded so rapidly during his career, and was quick to apply it to the understanding of his cherished insects. He was a showman who relished describing his insights and discoveries as colorfully as possible and was, as a consequence, a superb teacher and recruiter of young talent. Hundreds of leading insect researchers and teachers in this country and around the world were drawn to insects by Williams as undergraduates or graduate students, trained with him as post-doctoral fellows, or indirectly were influenced by him as next-generation students of his students.

My own recruitment to this circle occurred as an entering graduate student in September 1948, when Williams was in the early stages of his academic career. With little idea of who he was or what he studied, and with only an amorphous idea of my own goals, I was sent to his office for an interview. I emerged thirty minutes later, intensely excited, having accepted what turned out to be both my thesis problem and the first steps in a life-long career in the physiology of insect metamorphosis. The photograph accompanying this article portrays with great fidelity the outer force of the man who had appraised me, matched me to one of his current scientific obsessions, and proceeded to engage my allegiance.

The ambience of his laboratory during the 1940's and '50's was the very best of its era, and probably would be impossible to replicate at the present time. Each of us, including Williams, had a research project that resembled those of the others only in concerning an insect, and preferably a moth. Cocoon spinning, flight muscle mitochondria, endocrine gland transplantations, cytochrome fluctuations with metamorphosis, blood protein biochemistry, and ionic regulation of heart rates were all being studied as separate thesis topics. What held us together was a meeting with Williams over tea at the end of each day,



when we talked about each other's experiments, subjected his results to the same spirited scrutiny as our own, and served as an enchanted audience for his colorful and strongly opinionated conversations.

His most important early work dealt with the hormonal control of

pupal diapause and metamorphosis in the *Cecropia* silkworm—a subject that he worked by himself with neither technical nor student assistance. He spent Saturdays in his surgery anesthetizing pupae, cutting windows in their cuticle, transplanting tissues, and implanting chemicals, while a Red Sox game, in season, played in the background. His experiments complemented those elsewhere on other orders of insects in establishing how the prothoracic glands, corpora cardiaca, corpora allata, and the brain interact to control metamorphosis and molting. He was an innovative surgeon, and had astutely chosen the diapausing lepidopteran pupa as a system that would clearly distinguish between the roles of the hormones that interested him. His isolated pupal abdomen preparation was used to demonstrate, among other things, that the steroids crystallized by Karlson and Butenandt in 1952 were in fact the molting hormone secreted by the prothoracic glands. And he began the parade toward juvenile hormone identification with his demonstration in 1956 that ether extracts of the imaginal male abdomen of *Cecropia* were a rich source of corpus allatum activity.

In later years, as teams of biochemists followed in the wake of the pioneers of insect endocrinology, Williams became an advocate of the use of metamorphosis hormones and their analogues as pesticides, and of the study of plant-insect interactions mediated by these powerful substances. He played other roles as well, especially through his chairmanship of Biology at Harvard (which began a profound metamorphosis during his tenure), as chairman of the Section on Zoology of the National Academy of Science, and as consultant to chemical industries striving to develop new strategy insecticides.

Recalling Williams' extraordinarily productive career highlights the profound influence that the preoccupations of youth can have in shaping a career. The study of *Lepidoptera* provided not only an early arena for exercising his extraordinary gifts, but the roots that oriented and sustained his exceptional career.

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NOTICE TO CONTRIBUTORS

Contributions to the *Journal* may deal with any aspect of Lepidoptera study. Categories are Articles, Profiles, General Notes, Technical Comments, Book Reviews, Obituaries, Feature Photographs, and Cover Illustrations. Reviews should treat books published within the past two years. Obituaries must be authorized by the President of the Society. Requirements for Feature Photographs and Cover Illustrations are stated on page 111 in Volume 44(2). *Journal* submissions should be sent to the editor at the above address. Short manuscripts concerning new state records, current events, and notices should be sent to the *News*, Stephanie McKown, Editor, 650 Cotterell Drive, Boise, Idaho 83709 U.S.A. *Journal* contributors should submit manuscripts in *triplicate*, typewritten, *entirely double-spaced*, with wide margins, on one side only of white, letter-sized paper. Prepare manuscripts according to the following instructions, and submit them flat, not folded.

Abstract: An informative abstract should precede the text of Articles and Profiles.

Key Words: Up to five key words or terms not in the title should accompany Articles, Profiles, General Notes, and Technical Comments.

Text: Contributors should write with precision, clarity, and economy, and should use the active voice and first person whenever appropriate. Titles should be explicit, descriptive, and as short as possible. The first mention of a plant or animal in the text should include the *full scientific name with author, and family*. Measurements should be given in metric units; times in terms of the 24-hour clock (0930 h, not 9:30 AM). Underline only where *italics* are intended.

Literature Cited: References in the text of Articles, Profiles, General Notes, and Technical Comments should be given as Sheppard (1959) or (Sheppard 1959, 1961a, 1961b) and listed alphabetically under the heading LITERATURE CITED, in the following format without underlining:

SHEPPARD, P. M. 1959. Natural selection and heredity. 2nd ed. Hutchinson, London. 209 pp.

——— 1961a. Some contributions to population genetics resulting from the study of the Lepidoptera. *Adv. Genet.* 10:165–216.

Illustrations: Only half of symmetrical objects such as adults with wings spread should be illustrated, unless whole illustration is crucial. Photographs and drawings should be mounted on stiff, *white* backing, arranged in the desired format, allowing (with particular regard to lettering) for reduction to fit a *Journal* page. Illustrations larger than letter-size are not acceptable and should be reduced photographically to that size or smaller. The author's name and figure numbers as cited in the text should be printed on the *back* of each illustration. Figures, both line drawings and photographs, should be numbered consecutively in Arabic numerals; "plate" should not be employed. Figure legends must be typewritten, double-spaced, on a *separate sheet* (not attached to illustrations), headed EXPLANATION OF FIGURES, with a separate paragraph devoted to each page of illustrations. Color illustrations are encouraged; contact editor for submission requirements and cost.

Tables: Tables should be numbered consecutively in Arabic numerals. Headings for tables should not be capitalized. Tabular material must be typed on *separate sheets*, and placed following the main text, with the approximate desired position indicated in the text. Vertical lines as well as vertical writing should be avoided.

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CONTENTS

THE BUTTERFLIES OF ANAK KRAKATAU, INDONESIA: FAUNAL DEVELOPMENT IN EARLY SUCCESSION. <i>T. R. New and I. W. B. Thornton</i>	83
MASS FLIGHT RESPONSE OF OVERWINTERING MONARCH BUTTERFLIES (NYMPHALIDAE) TO CLOUD-INDUCED CHANGES IN SOLAR RADIATION INTENSITY IN MEXICO. <i>William H. Calvert, Lincoln P. Brower, and Robert O. Lawton</i>	97
LARVAL MORTALITY OF INDIAN TASAR SILKWORM (<i>ANTHERAEA MYLITTA</i>) (SATURNIIDAE) DUE TO PÉBRINE INFECTION. <i>C. S. K. Mishra, B. K. Nayak, and M. C. Dash</i>	106
SEXUAL DIFFERENCES IN HABITAT PREFERENCE AND BEHAVIOR OF <i>OENEIS CHRYXUS</i> (NYMPHALIDAE: SATYRINAE). <i>Dale L. Clayton and Daniel Petr</i>	110
BUTTERFLIES OF THE CAYMAN ISLANDS, WITH THE DESCRIPTION OF A NEW SUBSPECIES. <i>Lee D. Miller and Stephen R. Steinhäuser</i>	119
A NEW SPECIES OF <i>COLORADIA</i> FROM SONORA AND CHIHUAHUA, MEXICO (SATURNIIDAE: HEMILEUCINAE). <i>Claude Lemaire and Michael J. Smith</i>	128
BUTTERFLIES OF THE ARCHBOLD BIOLOGICAL STATION, HIGHLANDS COUNTY, FLORIDA. <i>Marc C. Minno</i>	138
GENERAL NOTES	
Occurrence of <i>Disphragis captiosa</i> (Notodontidae) in Arizona. <i>Ron Leuschner</i>	159
<i>Hileithia decostalis</i> (Crambidae: Pyraustinae), new to the United States. <i>Bryant Mather and Eugene Munroe</i>	159
A new lichen moth record for the United States: <i>Lycomorphodes sordida</i> (Arctiidae: Lithosiinae) from south Texas. <i>James K. Adams</i>	160
Life history notes on <i>Catocala sappho</i> and <i>Catocala ulalume</i> (Noctuidae). <i>Jeffrey R. Slotten</i>	161
BOOK REVIEWS	
Buggy books: A guide to juvenile and popular books on insects and their relatives. <i>Boyce A. Drummond</i>	164
Die raupen der schmetterlinge Europas. <i>Frederick W. Stehr</i>	166
A revision of the Indo-Australian genus <i>Attacus</i> . <i>Frederick H. Rindge</i>	166
A revision of the Indo-Australian genus <i>Attacus</i> . <i>Daniel H. Janzen</i>	167
OBITUARY	
Carroll Milton Williams. <i>William H. Telfer</i>	169

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589
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Volume 46

1992

Number 3

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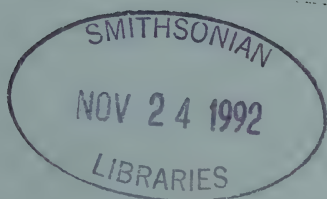
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Cover illustration: The painted lady, *Vanessa cardui* L. (Nymphalidae), is the most widespread butterfly species known. It occasionally exhibits mass dispersals involving thousands of individuals. Original illustration by Callie Mack, Natural Science Illustration, 8529 Jackie Drive, San Diego, California 92119.

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TEMPORAL CHANGES IN ABUNDANCE OF TWO LYCAENID BUTTERFLIES (LYCAENIDAE) IN RELATION TO ADULT FOOD RESOURCES

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ABSTRACT. The temporal distributions of adult *Hypochrysops apelles* (F.) and *H. epicurus* (Miskin) in relation to the abundance of flowering mangroves were examined over a 2.5 year period at Redland Bay near Brisbane, Australia. The flight period of both species (September to May) coincided with the flowering of two mangrove species that the butterflies visited for food. Within the flight period of *H. epicurus*, adult abundance was closely associated with the abundance of mangrove flowers over time. Several explanations for the observed relationship are suggested; the most likely causal factors are climate and adult food availability. A laboratory experiment confirmed that the availability of adult food (carbohydrate) could increase longevity in both species.

Additional key words: flight period, nectar, Australia, mangrove *Hypochrysops*.

Shapiro (1975) suggested that a butterfly's flight period depends primarily on the availability of sunshine, nectar, and oviposition sites. Given that these resources are available, predation and competition might then be important. Several studies have related the flight period of particular butterfly species to the availability of either favorable conditions for flight or suitable oviposition sites (Cappuccino & Kareiva 1985, Dobkin et al. 1987, Slansky 1974). However, the importance of nectar availability in determining the flight period of butterflies remains poorly studied.

There are indications that the temporal availability of flowers, together with seasonal and biological factors, may be important in determining the flight period of some butterfly species (Clench 1967, Owen 1971, Owen et al. 1972, Percival 1974, Shapiro 1975). Although these authors suggest that the temporal abundance of butterflies may be tied closely to the abundance of the flowers they utilize as adult food

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resources, their studies often have been based on anecdotal observations of flowering phenology. The aim of this study was to determine whether temporal changes in abundance of *Hypochrysops apelles* (F.) and *H. epicurus* Miskin were related to the temporal availability of their adult food resources. As such, it is one of the few attempts to obtain detailed temporal data on both butterflies and flowers and, while the observed associations are open to several interpretations, they represent a first step in determining whether such relationships exist.

METHODS

The study was conducted at Redland Bay (153°17'E, 27°35'S), situated on the coast of Moreton Bay near Brisbane, Australia. The climate is subtropical, with hot, wet conditions from October to March and mild, dry conditions from May to August. The study area comprised a patch of mangroves with an area of 14.7 hectares. The vegetation at the site is dominated by the mangrove *Avicennia marina* (Forssk.) Vierh (Avicenniaceae), but the mangroves *Rhizophora stylosa* Griff. (Rhizophoraceae), *Ceriops tagal* (Perrottet) C. B. Robinson (Rhizophoraceae), and *Aegiceras corniculatum* (L.) Blanco (Myrsinaceae) also are common.

In the Brisbane region, both *H. apelles* and *H. epicurus* are found only within mangrove habitats. However, at the northern end of its distribution, *H. apelles* occurs in a variety of other habitat types (Common & Waterhouse 1981). The larvae of *H. apelles* feed on the mature leaves of *R. stylosa* and *C. tagal*, although several other plant species have been recorded as hosts elsewhere (Common & Waterhouse 1981). *Hypochrysops epicurus* is restricted to mangrove habitats throughout its range (Common & Waterhouse 1981). The larvae of *H. epicurus* feed on the mature leaves of *A. marina*, which is the most abundant mangrove in the Brisbane region.

The abundance of the butterflies was estimated using a transect walk as described by Pollard (1977). The transect (which incorporated as much intra-habitat variation as possible) was 2100 m long and took an average of 95 minutes to complete. The sampling area was set at 10 m in front, 5 m on either side, and 5 m directly above the observer. Following Moore's (1975) technique, a long-handled butterfly net was waved over the vegetation in order to disturb any perching individuals. In order to encompass the period of maximum adult butterfly activity, observations were performed between 1030 h and 1430 h. To ensure that observations were carried out on days on which conditions were favorable for flight activity, the following criteria were adopted: (i) 50% or less of sample time spent under cloud cover, (ii) average tem-

perature between 17 and 32°C, and (iii) average wind speed of 10 km h⁻¹ or less. Any samples that did not fit these criteria were discarded.

The temporal availability of adult food was estimated by counting the number of flowering individuals (i.e., any plant that had flowers present) of all mangrove species for 5 m on either side of the transect. This method provides only a rough estimate of the amount of adult food available but accurately describes the time at which the food is available. In addition, records were kept of any feeding events by any butterfly species.

Sampling commenced in September 1982 and ceased in February 1985. Sampling was conducted once per month from September 1982 to August 1983 and from June 1984 to August 1984. From September 1983 to May 1984 and from September 1984 to February 1985, two sampling efforts per month were conducted.

In addition to the field sampling, a small laboratory experiment was conducted using adult *H. apelles* and *H. epicurus* reared from larvae collected in the field. In this experiment twelve to fourteen adult butterflies of each species were given either a water diet or a diet of 10% honey solution. The butterflies were kept in individual containers at a constant temperature of 25°C and a 12/12 hour light/dark cycle. Only longevity was measured because it was not possible to get either species to mate or lay eggs in the laboratory.

RESULTS

Avicennia corniculatum and *A. marina* were the only species whose flowers were visited by butterflies at Redland Bay. During this study *A. corniculatum* produced flowers from September to December, whereas *A. marina* flowered from January to April.

The temporal distribution of *H. apelles* was variable (Fig. 1). The flight period began in September and ended in May; however, the number of peaks in abundance varied from year to year. While the summer flight period coincided with the flowering of the two mangrove species used as adult food, no clear association between the butterfly and its adult food was observed within its flight period. Figure 2 presents the same data for *H. epicurus*. The flight period of *H. epicurus* commenced in September and finished in May with only two peaks of abundance evident. These peaks coincided with the flowering phenology of *A. corniculatum* and *A. marina*.

These trends are confirmed by correlations (Spearman's rank) between butterfly and flower abundance (Table 1). Both butterfly species were significantly correlated ($P < 0.01$) with flowering mangrove abun-

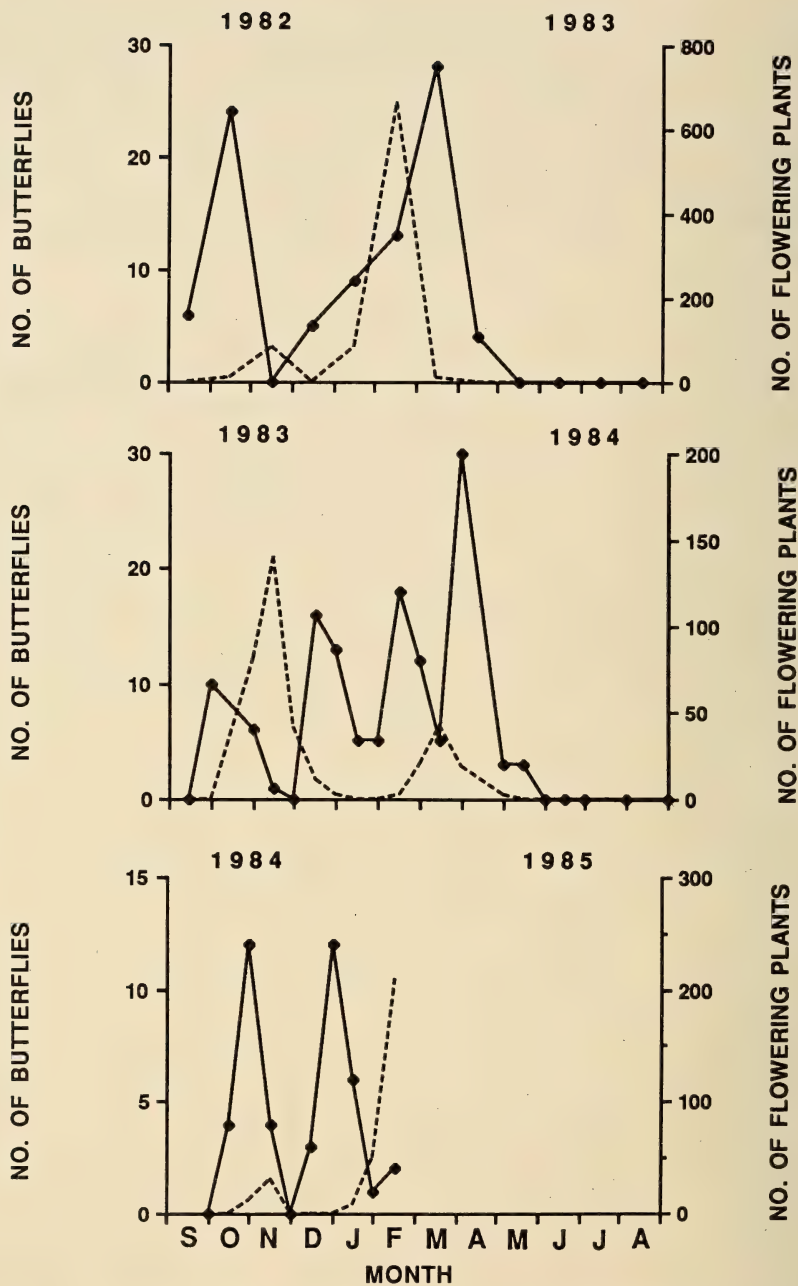


FIG. 1. Temporal changes in abundance of adult *H. apelles* (solid line) and the number of *A. corniculatum* and *A. marina* plants in flower (dashed line) from September 1982 to February 1985.

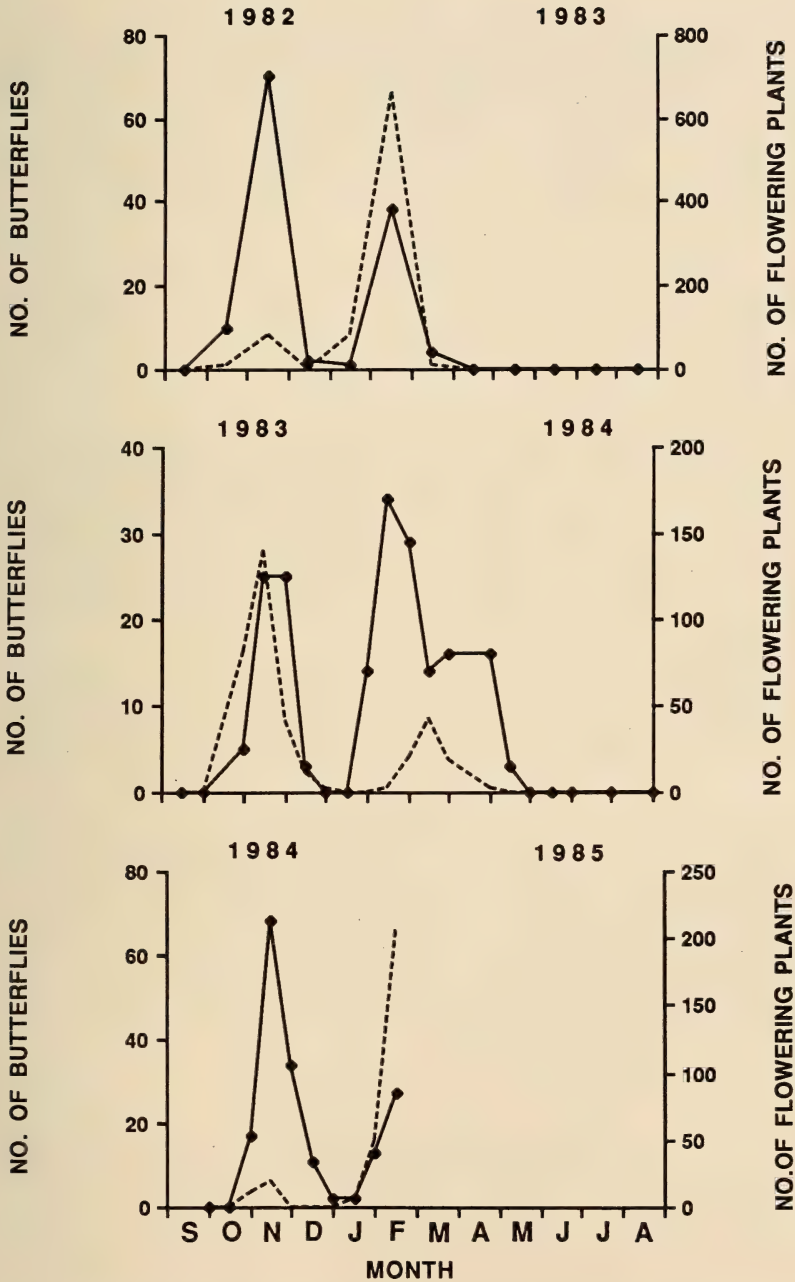


FIG. 2. Temporal changes in abundance of adult *H. epicurus* (solid line) and the number of *A. corniculatum* and *A. marina* plants in flower (dashed line) from September 1982 to February 1985.

TABLE 1. Correlations (Spearman's rank) between the abundance of adult *H. apelles* and *H. epicurus* and the number of flowering individuals of *A. corniculatum* and *A. marina* for samples occurring from September to May within the two complete sampling years and for all samples (NS: not significant; * $P < 0.05$; ** $P < 0.01$).

Species		Sep 1982– May 1983	Sep 1983– May 1984	Sep 1982– Feb 1985
<i>Hypochrysops apelles</i>	r^s	0.46	0.16	0.41
	n	9	16	42
	p	0.211 ^{NS}	0.559 ^{NS}	0.008*
<i>Hypochrysops epicurus</i>	r^s	0.68	0.62	0.70
	n	9	16	42
	p	0.042*	0.010*	0.001**

dance over the whole sampling period, indicating that the flight periods of the butterflies and the flowering of the mangrove species occurred in the same season from year to year. *Hypochrysops epicurus* abundance also illustrated a significant statistical correlation ($P < 0.05$) with the number of flowering mangroves within its flight period (September to May). *Hypochrysops apelles*, however, was not correlated with flowering mangroves within its flight period.

The results of the adult feeding experiment are given in Table 2. The availability of honey (carbohydrate and amino acids) in the adult diet greatly increased the longevity of both *H. apelles* and *H. epicurus*.

DISCUSSION

Although closely related and occupying similar habitats, *H. apelles* and *H. epicurus* exhibit different patterns of adult flight activity. Both species occurred as adults during the warmer months suggesting that climate plays a role in determining their flight period. In southeastern Queensland, all known *Hypochrysops* overwinter as mature larvae (D. Sands pers. comm.). Therefore, the start of the flight period in Septem-

TABLE 2. The mean longevity (days) and results of a *t*-test for adult *H. apelles* and *H. epicurus* provided with diets of either water or 10% honey solution.

Species	Diet	Mean longevity	Sample size	<i>t</i> -test
<i>H. apelles</i>	Water	3.0	12	6.7
	10% honey	20.2	13	$P < 0.001$
<i>H. epicurus</i>	Water	4.0	14	3.8
	10% honey	14.9	13	$P < 0.001$

ber commences when adults eclose from pupae produced by the overwintering larvae. Subsequent generations of adults result as the season progresses. In the case of *H. apelles*, the number of generations per year was variable, but for *H. epicurus* there were two distinct peaks of adult abundance each year. The close coincidence of the peaks of abundance shown by *H. epicurus* and the flowering of *A. corniculatum* and *A. marina* suggests that their respective phenologies are closely related.

There are three likely explanations for this temporal association between butterflies and flowers. First, the result may simply reflect the movement of butterflies into and out of the study site as flowers go into and out of bloom, as has been found for other species of lycaenids (Douwes 1975, Sharp & Parks 1973, Sharp et al. 1974). However, despite extensive searches of other nectar sources in the vicinity of the study site, neither species was observed outside the mangrove habitat.

Second, it is possible that larval resources in some way account for the observed flight periods. For instance, the nutritional quality of the mature leaves may vary throughout the year. *Hypochrysops epicurus* oviposits on the twigs of its larval food plant, and the larvae feed on mature leaves which are present throughout the year; therefore, this explanation seems unlikely. Alternatively, since the larvae of both species of butterfly are obligately tended by ants (Common & Waterhouse 1981), adult abundance may be related to ant activity. However, the appropriate ant species were observed on the mangroves at all times of the year, often tending overwintering larvae.

The final hypothesis is that the flight period and abundance of adult *H. epicurus* is timed to coincide with the availability of food resources in its habitat. The availability of food to adult butterflies can have important effects on the longevity and fecundity of some species (Leather 1984, Murphy et al. 1983, Norris 1935). The laboratory experiment on the effect of adult diet on *H. epicurus* and *H. apelles* demonstrated that the presence of honey in the diet greatly increased adult longevity of these species. In addition, Hill and Pierce (1989) have shown that the availability of sugar significantly increased both longevity and fecundity of the lycaenid *Jalmenus evagoras* (Donovan). Therefore, by maximizing longevity and fecundity, the availability of adult food has the potential to play an important role in the population biology of butterfly species. However, the temporal association between *H. epicurus* and the flowers on which it feeds may not be caused solely by a requirement of the adult butterflies for the sugars and/or amino acids in floral nectar. Butterfly species that are confined to mangroves are in a unique situation. If adults emerge during a period of the year in which no mangroves are flowering, then there are no alternative nectar

sources. Moreover, the mangrove substrate is highly saline and there is no source of water apart from rainfall. Therefore the mangrove flowers are the only predictable source of sugar, amino-acids, and water available to these butterflies. It is possible that the close temporal relationship between *H. epicurus* and flower abundance may be as much due to an avoidance of desiccation as to the availability of floral nectar as adult food. Watt et al. (1974) have stated that water may be as valuable a resource as nectar or excess pollen to flower visitors. In this respect, it is significant that the lycaenid butterfly *Acrodipsas illidgei* (Waterhouse and Lyell), another mangrove specialist found at the same site, is recorded as having a flight period from September to December and in February (Common & Waterhouse 1981, C. Hill unpubl. obs.). Thus, the flight period of this species coincides with the flowering times of the two mangrove species that are the major source of adult food for butterflies in this habitat. Even though *A. illidgei* are autogenous and do not require nectar to reproduce (Sands 1980), the availability of nectar might extend the longevity of adults.

In contrast to *H. epicurus*, *H. apelles* showed no close temporal association with its adult food. It may have alternative food sources that were unidentified in this study. Primack and Tomlinson (1978) have shown that *R. stylosa*, the larval food plant of *H. apelles*, secretes a sugar solution from its terminal leaves, but butterflies were not observed feeding on this secretion in this study. Alternatively, *H. apelles* may possess a life history strategy in which larval reserves provide sufficient energy throughout the length of the adult life.

To demonstrate unequivocally a temporal association between the flight period of a butterfly and the flowers that it uses as adult food resources requires the collection of several seasons' data in order to determine whether a pattern exists. The two and a half years' data collected in this study suggest that, for *H. epicurus*, the flight periods of the butterfly do coincide with the flowering of the mangroves that it uses as food. In addition, a laboratory experiment showed that the presence of sugar in the adult diet increased longevity. To test further this hypothesis would require some manipulation of the availability of adult food resources in the butterfly's habitat. Decreasing the temporal availability of adult food resources by removing key plant species would be an informative way to test such an hypothesis but also would be prohibitively destructive.

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GENITALIC CHARACTERIZATION, ENLARGEMENT, AND
REASSOCIATION OF THE NEOTROPICAL HESPERIINE
GENUS *HALOTUS* (HESPERIIDAE)

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ABSTRACT. Since classical characters involving facies, antennae, palpi, leg spines, wing shape, and venation do not, as previously used, rigorously delimit the genus *Halotus*, I do so using male genitalia. *Halotus* comprises three species: *H. angellus* (Plötz), the type, from at least Costa Rica and western Panama; *H. jonaveriorum* **new species** from Oaxaca, Mexico, which superficially looks like the type species; and *H. rica* (Bell) from southern Mexico to Costa Rica (and Ecuador?), which departs sharply from the other two species with respect to both facies and the male stigma. Mostly from male genitalia, I argue that *Halotus*, number 27 in Evans's (1955) 36-genus M or *Hesperia* group (the group most prevalent in the United States and Canada), relates to *Niconiades*, number 11 in his 20-genus O or *Calpododes* group. Evans's system of new world hesperiine generic groups is fatally flawed.

Additional key words: genitalia (male), stigma, taxonomy, generic groups, *Niconiades*.

I meant it when I wrote that "much of Evans's taxonomic system just below the level of the subfamily may be invalid" (Burns 1990:11). I was referring to his placement of 184 genera of American hesperiine skippers in 8 generic groups, lettered H to O (Evans 1955), and was extrapolating from the fact that *Amblyscirtes*, in his N or *Lerodea* group of 4 genera, belongs not with fellow groupies but with a few scattered genera in his 53-genus J or *Apauustus* group. Adding fuel to the fire, I argue here that genus *Halotus*, number 27 in Evans's 36-genus M or *Hesperia* group (the group most prevalent in the United States and Canada), relates to *Niconiades*, number 11 in his 20-genus O or *Calpododes* group.

Originally monotypic, *Halotus* is a small but growing genus that is strictly neotropical. Godman (1900:505) proposed it to accommodate a species (which he knew from two Costa Rican males) set off from external look-alikes by "the form of the brand [stigma]" and "the peculiar structure of the genitalia" (Fig. 1). Four decades later, Bell (1942) described a second species from a lone Costa Rican male, whose genitalia he figured but wrote nothing about. Because the upper side of its wings reminded Bell of *Atrytonopsis python* (Edwards), he put his new species in *Atrytonopsis*, whose genitalia differ greatly from those of *Halotus* (see Skinner & Williams 1924 [or Lindsey et al. 1931], Burns 1982, 1983). Evans (1955) correctly associated the two *Halotus* species, which differ substantially from each other in appearance. Now, half a century after Bell, I describe a third species from southern Mexico that super-

ficially looks like the first and genitally approximates the first in some respects, the second in others (while expressing its individuality).

I recharacterize the genus *Halotus* in terms of male genitalia (omitting female genitalia because females of two of the three species are lacking). The generic characters of Godman (1900) and Evans (1955) involve facies, antennae, palpi, leg spines, wing shape, and venation. As presented, these classical characters restrict the hesperiine field considerably but do not rigorously delimit *Halotus*.

Everyone wants to know about facies; but, because it can be so misleading, and because it has been so misread in the past, I play it down. In *Halotus*, as in so many other skippers, the ground color is dark brown, semihyaline spots variably relieve it in standard positions on the forewing (in spaces 2, 3, 6, 7, 8, and the cell), opaque spots sometimes mark the forewing (in space 1b) and dorsal hindwing (in spaces 2, 3, 4, 5, and the cell), and an elaborate system of opaque spots and overscaling creates a relatively complex ventral hindwing. (Bell [1942:4] thoroughly covers the ventral hindwing pattern in his description of *Halotus rica*.) What is far less common, the fringes of the wings are checkered in *Halotus* (see Figs. 14–19).

Judging from *H. rica* (the one species whose female I have seen), *Halotus* is not sexually dimorphic in color pattern. Although *Halotus* males do have a stigma on the dorsal forewing, its form is too inter-specifically variable (Figs. 11–13) to sharply define the genus.

In citing specimens, I place genitalic dissection numbers in brackets, museum abbreviations in parentheses. X-rated dissections are mine; the rest I credit individually. All dissected genitalia remain free in vials except those from the holotype of *Atrytonopsis rica* Bell, which are stuck on a slide. AMNH denotes the American Museum of Natural History, New York, N.Y.; USNM, the National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Halotus Godman, 1900

(Figs. 1–10)

Type species. *Hesperia angellus* Plötz (1886:94) = *Hesperilla saxula* Mabille (1891: LXXXI) = *Halotus saxula* Godman (1900:505, pl. 95, figs. 42–44).

Male genitalia. Overall, the tegumen, uncus, and gnathos look oddly squat (Figs. 2, 5, 8). The uncus is slightly divided (Figs. 2, 5, 8) and shorter than the gnathos (Figs. 1, 2, 3, 5, 6, 8, 9).

The outer side of the valva is simple; the inner side, complex. In lateral view, at about the middle of the posterior margin, a small rough point points backward; below this point, it looks as though the posteroventral corner of the valva were bitten off (Figs. 1, 3, 6, 9). In dorsal or, better, ventral view, almost the distal third of the valva presents an inwardly produced and wickedly toothed flange. In the paired valvae, these dentate flanges suggest jaws that could have taken the posteroventral bite out of those valvae (Figs. 4, 7, 10)! Arising dorsal to the flange, toward the top of each valva, a more or less oblong, distally dentate projection extends anteromediad (Figs. 1, 3, 4, 6, 7, 9, 10).

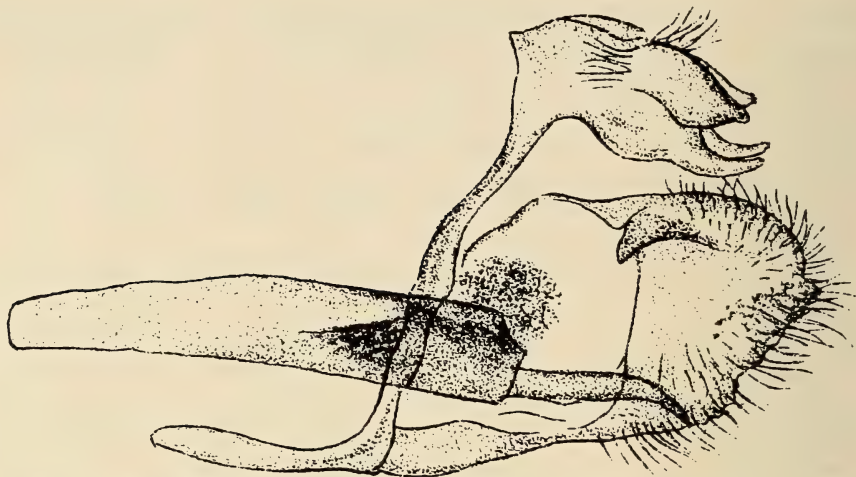


FIG. 1. Male genitalia of *Halotus angellus* from Irazú, Rio Sucio, COSTA RICA (ex Godman 1900:plate 95, fig. 44). Complete genitalia (minus left valva) in left lateral view. This figure presents the inner surface of the right valva whereas those that follow present the outer surface of the left valva.

The main body of the aedeagus, which is neither thick nor thin, is fairly uniform in diameter and fairly short—about three-fourths as long as the total intact genitalia (i.e., saccus plus valvae) (Figs. 1, 3, 4, 6, 7, 9, 10). The aedeagus ends ventrally in one or two robust, caudally directed, pointed prongs (Figs. 1, 3, 4, 6, 7, 9, 10). Its vesica carries three cornuti: a band of numerous spines, set in membrane, and two distinct, well-sclerotized units with one to several points (Figs. 3, 4, 6, 7, 9, 10). Myriad tiny spines crowd circumphallic membrane in a peculiar field just above the aedeagus (well above the juxta) (Figs. 3, 4, 6, 7, 9, 10).

The juxta lies ventral and lateral to the aedeagus, forming what amounts to an oblique U, but sits well back, quite hidden behind the valva, or valva plus vinculum, in lateral view (Figs. 3, 6, 9). Its transverse base has a concave anterior margin (Figs. 4, 7, 10), a pair of stubby, anteriorly- or anterolaterally-directed prongs at its anterolateral corners (Figs. 4, 7, 10), and a midventral, triangular projection (Figs. 4, 7, 10) that points anteroventrally (Figs. 3, 6, 9). On either side, two major lines of the U-shaped juxta cross in the narrowed zone where the ventral base connects with the broad, lateral arms (Figs. 3, 6, 9).

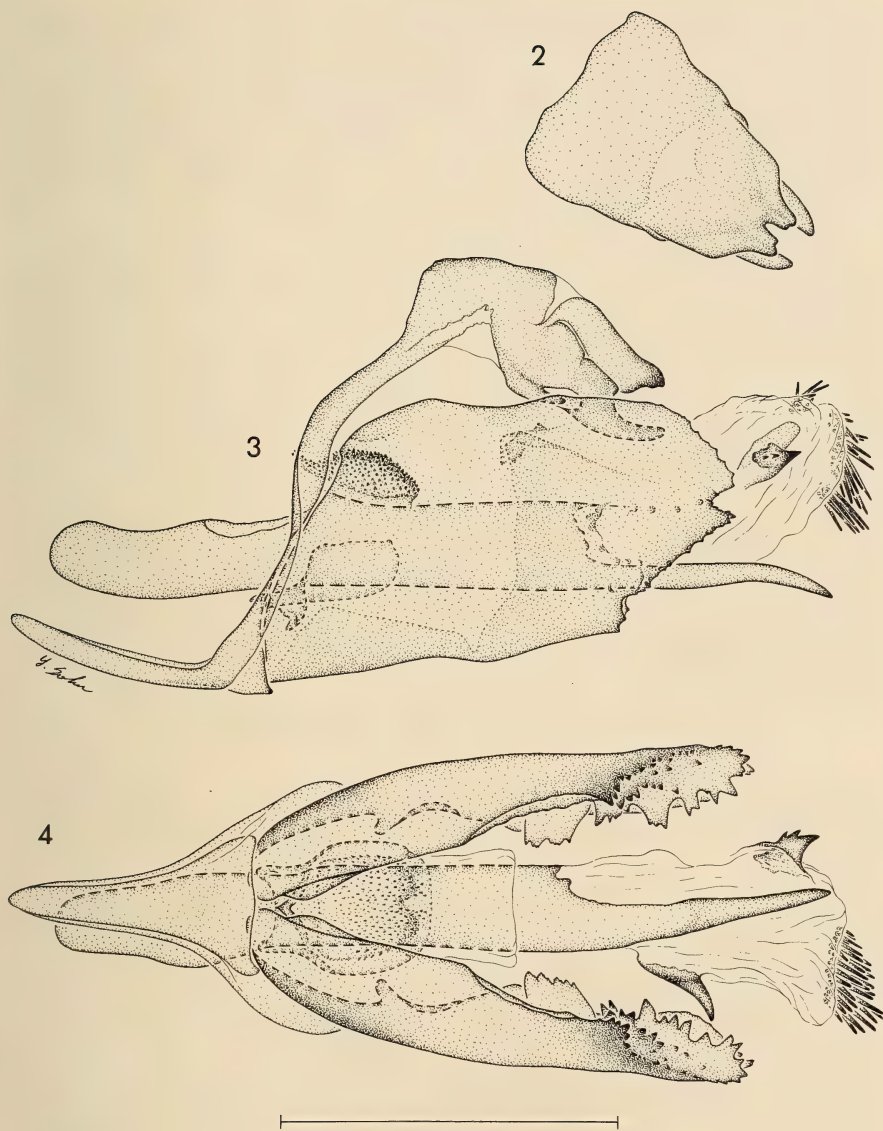
Geographic distribution. Middle elevations from southern Mexico (Jalisco, Puebla, Guerrero, Oaxaca, Chiapas) through Central America (Guatemala, El Salvador, Honduras, Costa Rica, western Panama [Chiriquí])—plus Ecuador (?).

Halotus angellus (Plötz)

(Figs. 1–4, 11, 14, 15)

Male genitalia (Figs. 1–4). Large gap between uncus and gnathos in lateral view (Figs. 1, 3). Each division of the divided uncus dual in dorsal view and slightly longer laterally than medially (Fig. 2).

In lateral view, rough point near middle of posterior margin of valva short and sharp (Figs. 1, 3). "Bite" out of ventrolateral corner of valva intermediate in depth and comparatively straight edged (Figs. 1, 3). Inwardly produced, wickedly dentate, "jawlike" flange set relatively high on valva—about midway between top and bottom of valva (Figs.



FIGS. 2-4. Male genitalia of *Halotus angellus* from Volcán Baru, 1800 m, Chiriquí, PANAMA, 5 December 1976, S. S. Nicolay [X-3089] (USNM). Scale = 1.0 mm. 2, Tegumen, uncus, and gnathos in dorsal view; 3, Complete genitalia (minus right valva) in left lateral view, with vesica everted (the simpler of the two discrete cornuti does not show at this angle); 4, Valvae, aedeagus (vesica everted to show cornuti), juxta, field of spines above aedeagus, saccus, and ventralmost vinculum in ventral view.

3, 4). Teeth on dorsal, oblong, anteromedially running projection of valva relatively coarse (Fig. 4).

One long prong at distal end of aedeagus on the right (Figs. 1, 3, 4). Cornutal spines larger and fewer (Figs. 3, 4) than in the other species of *Halotus*. The two discrete cornuti dissimilar: one a single, sharp, conspicuous point sprouting from one end of a low, elongate base (about like both of the discrete cornuti in *rica*); the other with multiple serrations sprouting from the middle of a low base (Figs. 3, 4). Field of numerous tiny spines above aedeagus at least as long as wide, and barely wider than aedeagus (Figs. 3, 4).

Midventral, triangular projection of juxta small (Figs. 3, 4).

Saccus the longest in the genus (Figs. 3, 4).

Stigma (Fig. 11). Inconspicuous. Bipartite: a triangular element in the angle between the cubitus and vein 2, not quite filling the apex of that angle; plus a linear element immediately below, along the lower side of vein 2.

Facies (Figs. 14, 15). Forewing cell and dorsal hindwing without spots. Semihyaline spots of forewing whitish or dirty white. That in space 2 usually shaped like > on the left and < on the right. Of the three small subapical spots in spaces 6, 7, and 8, only 7 always developed; and 6 more likely to dwindle than 8. Opaque spot in space 1b, just above vein 1, rudimentary to absent dorsally. Complex pattern of ventral hindwing mostly in shades of tan and brown and not contrasty.

Size (male forewing length). Mean 14.8 mm, range 14.0–15.4 mm, $n = 7$; the smallest species.

Type locality. Chiriquí.

Material examined. $n = 7$. COSTA RICA, Mount Poas, December, 2 ♂ [X-3088] (USNM).

PANAMA, CHIRIQUI: Volcán, 1465 m, 23 August 1964, 2 ♂, G. B. Small [H 304, S. S. Nicolay] (USNM); 30 June 1965, 1 ♂, G. B. Small (USNM). Volcán Baru, 1800 m, 5 December 1976, 2 ♂, S. S. Nicolay [X-3089] (USNM).

Steinhauser (1975) lists 15 ♂ of *H. angellus* from a single locality in western El Salvador. I do not know whether they belong to this species or the next.

Halotus jonaveriorum, new species

(Figs. 5–7, 12, 16, 17)

Male genitalia (Figs. 5–7). Large gap between uncus and gnathos in lateral view (Fig. 6), as in *angellus*. Each division of the divided uncus dual in dorsal view but slightly longer medially than laterally (Fig. 5)—and therefore visibly dual in lateral view, as well (Fig. 6).

In lateral view, rough point near middle of posterior margin of valva short and truncate (Fig. 6). "Bite" out of ventrolateral corner of valva comparatively deep and curved (Fig. 6). Inwardly produced, wickedly dentate, "jawlike" flange set relatively low on valva—closer to bottom than top of valva (Figs. 6, 7). Teeth on dorsal, oblong, anteromedially running projection of valva relatively fine (Fig. 7).

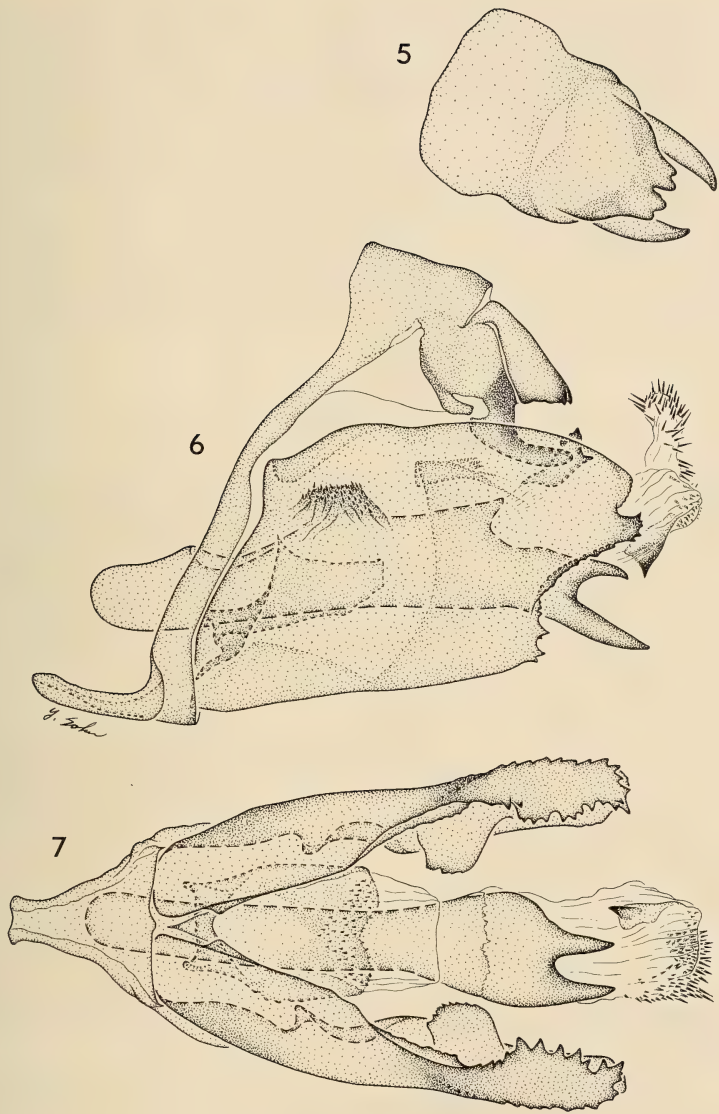
Two short prongs at distal end of aedeagus, one (lower) in the center and one (higher) on the right (Figs. 6, 7); central prong longer and directed noticeably downward (Fig. 6). Cornutal spines smaller and more numerous (Figs. 6, 7) than in *angellus*. The two discrete cornuti dissimilar: one with one or more short serrations sprouting from one end of a small, low base; the other with multiple serrations sprouting sharply along one side of a large, low base (Figs. 6, 7). As in *rica*, field of numerous tiny spines above aedeagus wider than long, and much wider than aedeagus (Figs. 6, 7).

Midventral, triangular projection of juxta large and more anteroventrally oriented than in *angellus* and *rica* (Figs. 6, 7).

Saccus the shortest in the genus (Figs. 6, 7).

Stigma (Fig. 12). Inconspicuous. Bipartite: a triangular element in the angle between the cubitus and vein 2, not quite filling the apex of that angle; plus a linear element immediately below, along the lower side of vein 2. All as in *angellus*.

Facies (Figs. 16, 17). Very like *angellus*. Forewing cell and dorsal hindwing without spots. Semihyaline spots of forewing dirty white to vaguely yellowish. That in space 2 somewhat suggestive of > on the left and < on the right, especially ventrally, but less



FIGS. 5-7. Male genitalia of *Halotus jonaveriorum*, holotype, from La Soledad-Buena Vista, Sierra Madre del Sur, 1525 m, Oaxaca, MEXICO, 12 April 1990, J. Kemner [X-2970] (USNM). Scale = 1.0 mm. **5**, Tegumen, uncus, and gnathos in dorsal view; **6**, Complete genitalia (minus right valva) in left lateral view, with vesica everted to show cornuti; **7**, Valvae, aedeagus (vesica everted—the fancier of the two discrete cornuti does not show at this angle), juxta, field of spines above aedeagus, saccus, and ventralmost vinculum in ventral view.

than in *angellus* because the apex tends to fill in to make a triangular instead of angular spot. Of the three small subapical spots in spaces 6, 7, and 8, only 7 always developed. Small, linear, opaque yellow spot in space 1b dorsally, just above vein 1. Complex pattern of ventral hindwing mostly in shades of tan and brown and not contrasty.

Size (male forewing length). Mean 15.6 mm, range 14.5–17.2 mm, $n = 11$; the middle species.

Material examined. Holotype: MEXICO, OAXACA, Sierra Madre del Sur, La Soledad-Buena Vista, 1525 m, 12 April 1990, ♂, John Kemner [X-2970]; deposited in the National Museum of Natural History, Smithsonian Institution (USNM).

Paratypes: 10 ♂ taken by John Kemner at the type locality as follows: 12 April 1990, 1 ♂; 16 April 1990, 1 ♂; 6 May 1990, 2 ♂ [X-3243]; 21 November 1990, 4 ♂ [X-3078, X-3079, X-3244]; 2 December 1991, 2 ♂ (4 in the collection of H. A. Freeman, 6 in USNM).

Etymology. I am delighted to name this species for both John Kemner who collected all the material and H. Avery Freeman who spread it and passed it on. I have deliberately dropped the surname and "h" from each.

Halotus rica (Bell) (Figs. 8–10, 13, 18, 19)

Male genitalia (Figs. 8–10). Little or no gap between uncus and gnathos in lateral view (Fig. 9). Uncus comparatively narrow at its distal tip (Fig. 8). Each division of the very shallowly divided uncus (Fig. 8) dual in lateral view, with the subdivisions one above the other (Fig. 9) instead of side by side as in *angellus* and *jonaveriorum*.

In lateral view, rough point near middle of posterior margin of valva somewhat long and sharp; posterior margin above it more nearly straight and vertical (Fig. 9). "Bite" out of ventrolateral corner of valva comparatively shallow and straight edged (Fig. 9). Inwardly produced, wickedly dentate, "jawlike" flange set relatively low on valva—much closer to bottom than top of valva (Figs. 9, 10). Teeth on dorsal, oblong, anteromedially running projection of valva relatively coarse (Fig. 10).

Two short prongs at distal end of aedeagus, one (lower) on the left and one (higher) on the right (Figs. 9, 10); both (especially the right) curved gently downward (Fig. 9). Cornutal spines smaller and more numerous (Figs. 9, 10) than in *angellus*. The two discrete cornuti similar: each a single, sharp, conspicuous point sprouting from one end of a low, elongate base; base narrower in one cornutus than in the other (Figs. 9, 10). Field of numerous tiny spines above aedeagus wider than long, and much wider than aedeagus (Figs. 9, 10).

Midventral, triangular projection of juxta small (Figs. 9, 10).

Saccus intermediate in length (closer to *angellus*) (Figs. 9, 10).

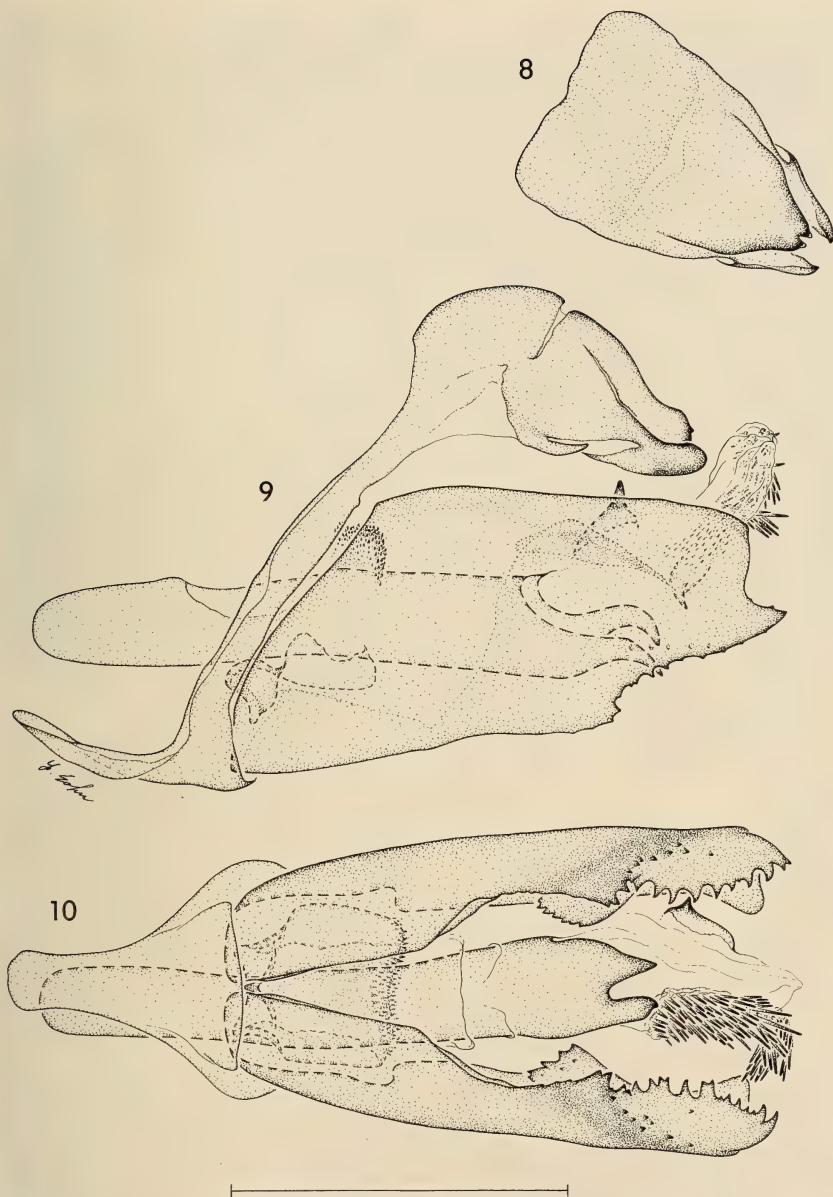
Stigma (Fig. 13). A little less inconspicuous than in *angellus* and *jonaveriorum*. Tripartite: a linear element running along the lower side of the cubitus from the origin of vein 3 to a point about half way toward the origin of vein 2, where it bends to cross space 2; a large spot immediately below, against the lower side of vein 2 in the top of space 1b; and a smaller spot just below that in about the middle of space 1b. Quite different from *angellus* and *jonaveriorum*.

Facies (Figs. 18, 19). Forewing cell with a dual semihyaline spot and dorsal hindwing with a total of five opaque yellowish orange spots—small and round in the cell but large and long in spaces 2, 3, 4, and 5 (the last two more or less fused). Semihyaline spots of forewing light yellowish orange. That in space 2 large and quadrate. Of the three subapical spots in spaces 6, 7, and 8, 6 and 7 always developed. Large, linear, opaque yellowish orange spot in space 1b dorsally, just above vein 1. Complex pattern of ventral hindwing mostly in shades of grayish white and brown and therefore contrasty. Relative to *angellus* and *jonaveriorum*, a well marked and jazzy skipper.

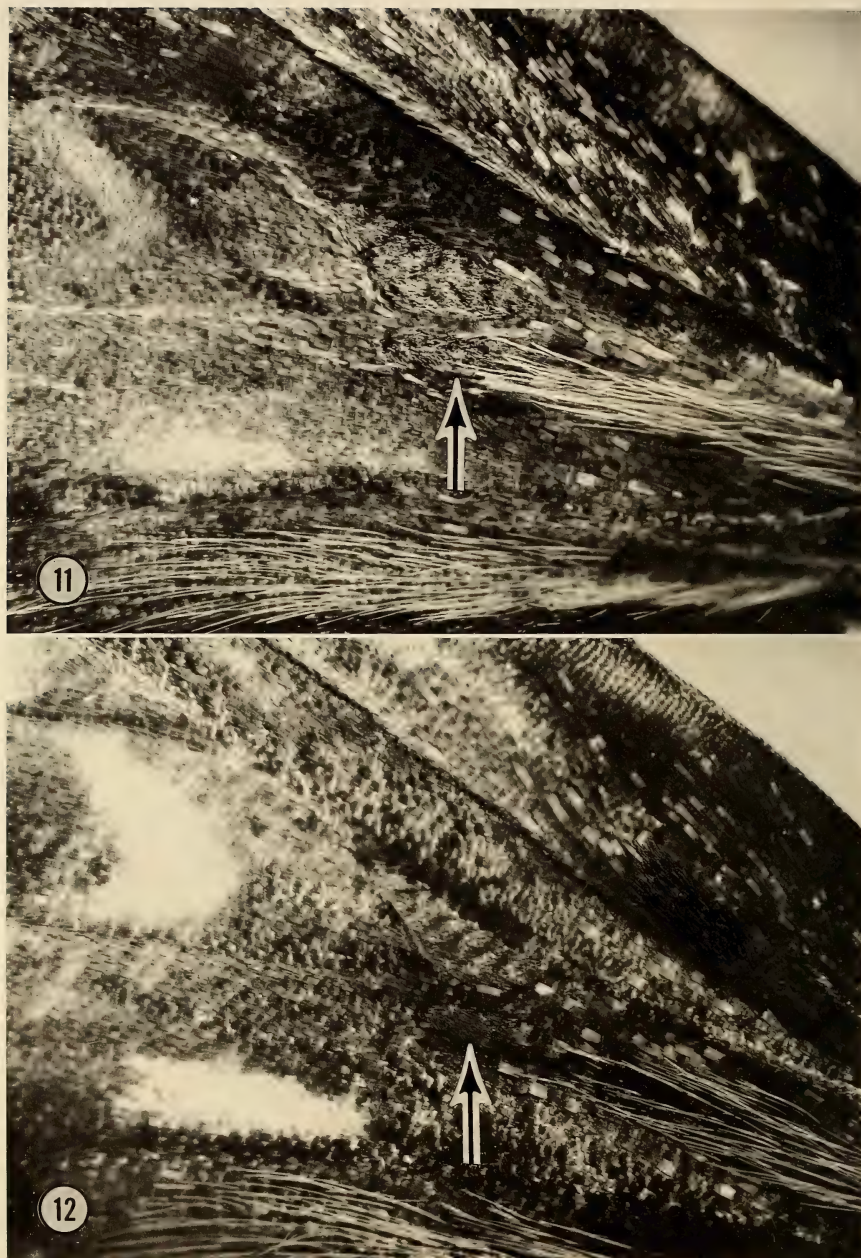
Size (male forewing length). Mean 17.1 mm, range 15.9–17.8 mm, $n = 4$; the largest species.

Type locality. Costa Rica.

Material examined. $n = 11$. MEXICO: JALISCO, Guadalajara, 1 ♂ [X-2332] (USNM). PUEBLA, Dos Caminos, 1220 m, July 1991, 1 ♂, M. Rangel [X-3245] (USNM). GUER-



FIGS. 8-10. Male genitalia of *Halotus rica* from El Zamorano, HONDURAS, 10 July 1980, R. D. Lehman [X-2404] (USNM). Scale = 1.0 mm. **8**, Tegumen, uncus, and gnathos in dorsal view; **9**, Complete genitalia (minus right valva) in left lateral view, with vesica everted to show cornuti; **10**, Valvae, aedeagus (vesica everted—one of the two discrete cornuti does not show at this angle), juxta, field of spines above aedeagus, saccus, and ventralmost vinculum in ventral view.



FIGS. 11, 12. Bipartite male stigmas of *Halotus*: upper, triangular element is well to the right of the semihyaline angular to triangular spot in space 2 and lower, linear element (marked by arrow) is just across vein 2 in upper part of space 1b, well above and to the right of the opaque spot (in space 1b) which lies just above vein 1 of the left forewing. From specimens in Figs. 14-17. 11, *H. angellus*; 12, *H. jonaveriorum*, holotype.

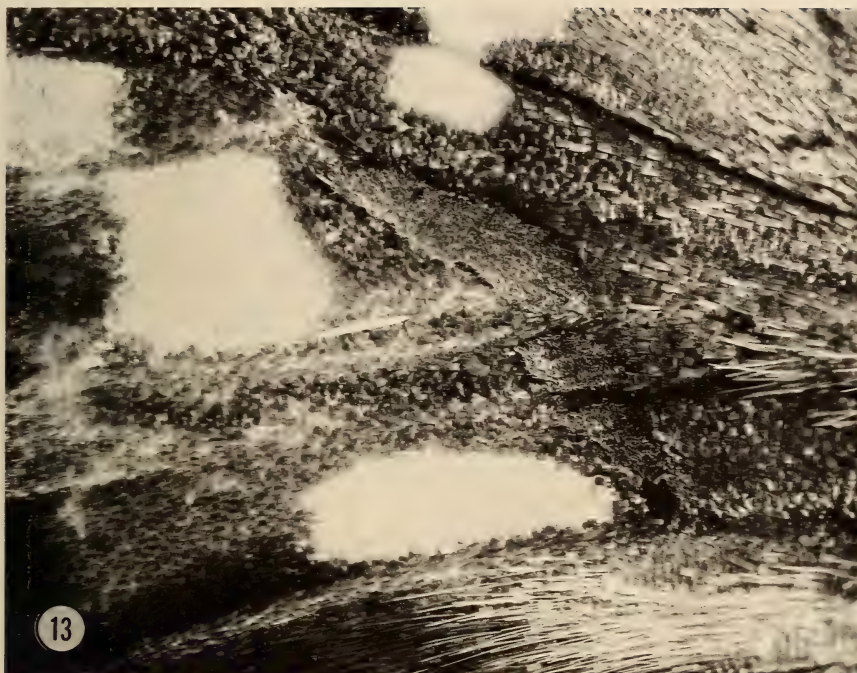


FIG. 13. Tripartite male stigma of *Halotus rica* extending from near the upper right corner of the quadrate semihyaline spot in space 2 almost to the right end of the opaque spot (in space 1b) which lies just above vein 1 of the left forewing. From specimen in Figs. 18, 19.

RERO, Acahuizotla, September 1960, 1 ♂, T. Escalante [H-660, H. A. Freeman] (AMNH). OAXACA, Oaxaca, 22 June 1966, 1 ♀, H. A. Freeman (AMNH). CHIAPAS: Muste, 24 August 1968 and 11 September 1968, 2 ♂, E. C. Welling (AMNH); San Jeronimo, vicinity Tacana Volcano, 450 m, 9 September 1970, 1 ♂, E. C. Welling (AMNH).

EL SALVADOR, Cojutepeque, 7 July 1952, 1 ♂ (USNM).

HONDURAS, El Zamorano, 10 July 1980, 1 ♂, R. D. Lehman [X-2404] (USNM).

COSTA RICA: 1 ♂ (holotype) [G 1130, E. L. Bell] (AMNH). San José, 13–18 November 1977, 1 ♀, W. H. Wagner [X-3246] (USNM).

Evans (1955:362) lists "1 ♀ Guatemala. 1 ♂ Ecuador (Zamora)" for *H. rica* in the collection of the British Museum (Natural History). Because the Ecuadorian male is the only specimen of *Halotus* I know of from south of Chiriquí, Panama, verification is desirable; but, because *Halotus* is still poorly represented in collections, the record may be real.

Reassociating *Halotus*

Evans (1955) makes *Halotus* the last genus in what is by far the largest division (the 22-genus *Hesperia* subgroup) of his 36-genus M or *Hesperia* group. In addition to *Hesperia*, this subgroup contains such familiar genera to American collectors as *Atalopedes*, *Polites*, *Wallengrenia*, *Atrytone*, *Poanes*, *Ochlodes*, and *Paratrytone*. I have been closely studying the genitalia of these skippers, particularly during the



FIGS. 14-19. Males of *Halotus* in dorsal (even numbered) and ventral (odd numbered) view (all $\times 1$). 14, 15, *H. angellus* from Volcán Baru, 1800 m, Chiriquí, PANAMA, 5 December 1976, S. S. Nicolay (USNM); 16, 17, *H. jonaveriorum*, holotype, from La Soledad-Buena Vista, Sierra Madre del Sur, 1525 m, Oaxaca, MEXICO, 12 April 1990, J. Kemner [X-2970] (USNM); 18, 19, *H. rica*, from El Zamorano, HONDURAS, 10 July 1980, R. D. Lehman [X-2404] (USNM).

past six years (Burns 1985, 1987, 1989, 1992, unpubl.), and see no special similarity between them and those of *Halotus*.

However, I do see similarities between the genitalia of *Halotus* (Figs. 1-10) and those of another neotropical genus, *Niconiades*, which is the last genus in the largest division (the 7-genus *Niconiades* subgroup) of Evans's (1955) 20-genus O or *Calpodus* group. Although the rough general resemblance, in itself, might not be significant, it is bolstered by specifics. *Niconiades*, like *Halotus*, produces a dentate, inwardly directed flange from the inner side of the distal part of the valva. In both genera, the aedeagus ends in one or two caudally directed, pointed prongs that range from short to long. Almost all species of *Niconiades* express the peculiar field of spines in membrane just above the aedeagus and well above the juxta (these crowded spines are larger in *Niconiades* than they are in *Halotus*). In my genitalic characterization of *Halotus*, the entire paragraph describing the juxta applies nearly as well to *Niconiades* (in *Niconiades*, the juxta is still more posterior than it is in *Halotus*, and the anterior margin of its transverse base is sometimes convex instead of concave).

I do not yet know enough about the genitalia of neotropical hesperiines across the board to say how close *Halotus* and *Niconiades* really

are. *Niconiades* differs strongly (and consistently) from *Halotus* in the form and also the length of the uncus (longer, instead of shorter, than the gnathos) and lacks cornuti, which are so characteristic in *Halotus*. A much larger genus, *Niconiades* varies much more in valval shape.

With respect to several classical nongenitalic characters, *Halotus* and *Niconiades* are not so different as wing shape and facies might at first suggest. (Facies is especially tricky to interpret since it shifts abruptly within each genus—in *Halotus*, compare *angellus* and *jonaveriorum* [Figs. 14–17] with *rica* [Figs. 18, 19]; *Niconiades* makes a bigger jump than that. Some *Niconiades*, like all *Halotus*, have checkered wing fringes.) Stigmas of *Niconiades* vary from bi- to tripartite (though not in the way that they do in *Halotus*). When bipartite, they usually resemble or exactly copy (in both form and position) the bipartite stigmas of *H. angellus* and *H. jonaveriorum* (Figs. 11, 12); and when tripartite, the upper two elements keep the bipartite positions on the wing. Antennae of *Halotus* are relatively longer, with less chunky clubs, than those of other *Hesperia* subgroup genera and hence are much like those of *Niconiades* (the nudum is shorter in *Halotus* [11 to 13 segments, distributed 3/8 to 4/9] than it is in *Niconiades* [13 to 16 segments, distributed 5/8 to 7/9]). Palpi are remarkably similar in *Halotus* and *Niconiades*.

Because these—and other (Burns 1990)—related genera are far apart in Evans's (1955) system, it is fatally flawed. In that connection, it is abundantly and painfully clear to me that *Niconiades* is nowhere near other genera in Evans's *Niconiades* subgroup such as *Thespies*, *Vacerra*, and *Oxyntes*, and, furthermore, that *their* closest relatives are widely scattered in at least three major generic groups of Evans besides M and O—but that is another story.

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FOODPLANT SPECIFICITY AND BIOLOGY OF
OIDAEMATOPHORUS BALANOTES (PTEROPHORIDAE):
A NORTH AMERICAN MOTH INTRODUCED INTO
AUSTRALIA FOR THE BIOLOGICAL CONTROL OF
BACCHARIS HALIMIFOLIA

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ABSTRACT. The stem-boring moth, *Oidaematophorus balanotes* (Meyrick) (Pterophoridae), was investigated as a biological control agent for *Baccharis halimifolia* L. (Asteraceae), an introduced weed in Australia. *Oidaematophorus balanotes* occurs from New York to the Rio Grande Valley and its larval hosts are *B. halimifolia* and *B. neglecta* Britton. It is univoltine throughout its range except in Florida where there may be two overlapping generations per year. The host range of *O. balanotes* was determined by observing the response of moths and neonate larvae on 64 economically important plants and *B. halimifolia*. In multiple choice tests, moths oviposited almost exclusively on *B. halimifolia*. Larvae placed on foliage of the test plants were able to complete development only on *B. halimifolia*. As a result, *O. balanotes* was considered safe for release in Australia where it was established in southeastern Queensland in 1985.

Additional key words: Asteraceae, host plant, Florida, Texas.

The woody shrub *Baccharis halimifolia* L. (Asteraceae: Astereae: Baccharidinae), an introduction from North America, is a serious weed in Queensland, Australia (Stanley & Ross 1986, Palmer 1987). The Queensland Department of Lands, through the Alan Fletcher Research Station, therefore initiated a long-range research program in 1960 to find biological control agents in the New World for release against this weed in Australia. Following initial surveys by F. D. Bennett (Palmer & Bennett 1988), officers of the Alan Fletcher Research Station, including the second author, commenced a three year research program in 1967 at the Archbold Research Station, Lake Placid, Florida, to determine the host specificity of selected insects. In the next decade, efforts focused on South American fauna but in 1982 the North American Field Station was established to continue work in the North American region.

The genus *Baccharis* is one of the largest in the Astereae, with approximately 450-500 species, all of which are native to the New World (Nesom 1990). About 90% of the species occur in South America (Nesom 1990); twenty species occur in the United States (Mahler & Waterfall 1964). Nesom (1990) divided the 43 species occurring in North and

Central America into six sections. *Baccharis halimifolia* was nominated as the type species of the section *Baccharis*. Other species of relevance to this study that were placed in this section include *B. angustifolia* Michx., *B. dioica* Vahl, *B. glomerifolia* Pers., and *B. neglecta* Britt. *Baccharis sarathroides* Gray was placed by Nesom (1990) in the section *Sergilae*, which is very closely related to the section *Baccharis*.

The insect fauna on *B. halimifolia* has been described by Palmer (1987) and Palmer and Bennett (1988). One of the first insects selected in 1967 for further study at Lake Placid was the moth, *Oidaematophorus balanotes* (Meyrick) (Pterophoridae), larvae of which frequently were found boring in the stems of *B. halimifolia* and occasionally causing considerable damage to the shrub. Moreover, search of the literature, examination of previously collected specimens, and observation of surrounding flora suggested that *O. balanotes* larval foodplant range might be confined to *Baccharis* spp.

Oidaematophorus balanotes

Taxonomy

Oidaematophorus Wallengren is a large genus containing 73 species (Hodges et al. 1983). Within this genus, the *balanotes* group (Cashatt 1972) includes *O. balanotes*, *O. grandis* (Fish), *O. lacteodactylus* (Chambers), *O. kellicottii* (Fish), and *O. glenni* Cashatt.

Until the revision of the group by Cashatt (1972), who examined the genitalia of both sexes, these species were very difficult to separate. Indeed, specimens collected from *B. halimifolia* prior to 1972 were frequently identified as either *O. balanotes*, *O. kellicottii*, or *O. lacteodactylus*. We now believe that these specimens were most probably *O. balanotes*.

Distribution and Larval Food Plant Range

Although some adults have been captured in Arizona, *O. balanotes* is essentially an eastern species (Cashatt 1972) that occurs along the eastern seaboard from New York in the north to the Rio Grande Valley in Texas. This distribution approximates that of its *Baccharis* hosts.

The first author has collected larvae of *O. balanotes* from *B. halimifolia* and *B. neglecta* on many occasions (Palmer 1987). Almost certainly it also occurs on the Florida species *B. glomeruliflora* and *B. angustifolia*. Its host in Arizona is probably *B. sarathroides*.

Cashatt (1972) gives *Myrica* sp. (Myrtaceae) as a larval host based on one specimen record in the material he examined. However, we believe that this record is in error. *Myrica* and *B. halimifolia* are similar looking shrubs growing in the same habitat and sharing the same com-

mon name, "sea myrtle". Apart from this one record, *Baccharis* spp. are the only known hosts for *O. balanotes* (Cashatt 1972).

Indeed, all species in the *balanotes* group appear to have very narrow larval host ranges within the tribe Astereae. *Oidaematophorus grandis* has been collected from *B. pilularis* (Cashatt 1972); *O. kellicotti* from *Solidago* (Cashatt 1972), *B. neglecta*, and *B. dioica* (Palmer unpubl. data); *O. lacteodactylus* from *Solidago* sp. (Cashatt 1972); and *O. glenni* from *Solidago canadensis* (Cashatt 1972).

Biology and Phenology

The moths are rather delicate with brownish white wings spanning about 40 mm. Females oviposit eggs singly on the leaves, leaf axils, young twigs, and probably inflorescences. The eggs are oval, 0.5 mm long, and translucent white. Accurate egg counts were not made but we estimate that a female might produce a brood of several hundred eggs.

Larvae feed initially on leaves, inflorescences, and young stems. Although pterophorids are not known to be leaf miners, early instar *O. balanotes* tunnel into leaves to feed on the mesophyll. After a few days they move to the stem, either at the leaf axil or at the terminal, enter, and then feed for two to three weeks. A further migration then occurs as the larvae seek out more mature tissues further down the stems. Tunnels are made in mature stems of more than a year in age and these may reach over a meter in length. The entrance to this tunnel remains open although surrounded by a characteristic, granular frass. The larva is similar to that of *O. grandis*, which was described by Peterson (1962), except that the granulated texture of the anal shield is more uniform. Both of these species have two "urogomphi-like" hooks present on the anal shield, a character present only on very few Lepidoptera species. Larvae pupate in the tunnel and the moth emerges through the tunnel opening.

Throughout most of its range there appears to be one generation a year with moths emerging over summer. Early instars are found in autumn and often can be collected from inflorescences. Terminal twig death of the hosts occurs as these early instars attack new growth of stem tips. Tunnelling in more mature tissue then commences and the larvae overwinter in these tunnels. Larval tunnelling continues in the spring until the larvae pupate.

In Florida, where the winter is less pronounced, there appear to be two generations a year and the generations are not discreet. For example, in central Florida in February 1983, all stages from early instars to mature pupae were found in the stem tunnels.

Four species of hymenopteran parasitoids were reared from the lar-

vae: three Braconidae: *Macrocentrus cerasivoranae* Vierick, *Chelona* sp., *Chelonus* (*Microchelonus*) sp.; and one Ichneumonidae: *Temelucha cartipetiolata* Dasch. Parasitism rates ranged from 40–60% with *M. cerasivoranae* being the most abundant species.

Host Plant Specificity

Oviposition preference. Oviposition behavior was tested by randomly assigning each of two potted plants of 64 test plant species (Table 1) to one of eight cages. *Baccharis halimifolia* was included as a control in all eight cages. Twenty unsexed moths were released into each cage and honey-water wicks were placed in the cages for their nourishment. After five days, when the control plants were infested with eggs, the cages were dismantled and all eggs on the potted plants and cage walls were counted. The plants then were transferred to a greenhouse and observed until feeding was seen on the *B. halimifolia* controls. All plants were then reexamined for evidence of larval feeding.

Plants of *B. halimifolia* in all cages had dozens of eggs attached. Only five other plant species had eggs: *Leucaena leucocephala* (Lam.) de Wit., *Cucumis melo* L., and *Triticum aestivum* L. each had one egg; one plant of *Carica papaya* L. had seven eggs; both plants of *Paspalum dilatatum* Poir had one egg. The foliage of all these plants was in close proximity to that of *B. halimifolia*. On no other plant were eggs or feeding damage found. Hatch rate of eggs on *B. halimifolia* was greater than 80% and feeding on the plant tips and boring into the stems were seen on all these plants. The eggs on all the other plants hatched but no feeding occurred. We conclude that *O. balanotes* is highly selective about its choice of larval food plants, that oviposition of a few eggs laid on other plants probably was an artifact of caging, and that, of the plants tested, only *B. halimifolia* is a suitable host.

Larval feeding. Moths confined in cages with *B. halimifolia* plants oviposited, after which leaves with eggs were cut into sections so that each section contained 4 eggs. These leaf sections were then glued to the leaves of the test plants (Table 1), which were arranged in groups of eight with one *B. halimifolia* plant as a control. There were two replications of each plant species except sunflower, *Helianthus annuus* L., which had seven replications. Eggs hatched normally with a hatching rate above 95%. After 5 weeks, when vigorous larval tunnelling was seen in the controls, all plants were examined carefully.

Eggs hatched and larvae developed normally on all *B. halimifolia* plants. In most cases feeding was seen immediately below the eggs. In other cases larvae moved up to 50 mm from the egg to enter the leaf petiole, leaf axil, or the stem. With one exception, larvae made no attempt to feed on any test plant; no tissue abrasions could be seen

TABLE 1. Plant species tested as potential hosts of *Oidaematophorus balanotes*.

Apiaceae: <i>Daucus carota</i> L.; <i>Pastinaca sativa</i> L.
Anacardiaceae: <i>Mangifera indica</i> L.
Asteraceae: <i>Baccharis halimifolia</i> L.; <i>Carthamus tinctorius</i> L.; <i>Chrysanthemum</i> sp.; <i>Dahlia</i> sp.; <i>Helianthus annuus</i> L.; <i>Lactuca sativa</i> L.
Brassicaceae: <i>Brassica oleraceae</i> (L.) Alef.; <i>Brassica rapa</i> L.
Bromeliaceae: <i>Ananas comosus</i> (L.) Merr.
Caricaceae: <i>Carica papaya</i> L.
Chenopodiaceae: <i>Beta vulgaris</i> L.
Convolvulaceae: <i>Ipomoea batatas</i> (L.) Lam.
Cucurbitaceae: <i>Cucumis melo</i> L.; <i>Cucumis sativus</i> L.; <i>Cucurbita maxima</i> Duch.
Fabaceae: <i>Arachis hypogaea</i> L.; <i>Centrosema pubescens</i> Benth. <i>Desmodium canum</i> (Gmel.); <i>Glycine wightii</i> (R. Grah. ex Wight & Arn.) Verdc.; <i>Glycine max</i> (L.) Merr.; <i>Medicago sativa</i> L.; <i>Phaseolus atropurpureus</i> DC.; <i>Phaseolus vulgaris</i> L.; <i>Pisum sa-</i> <i>tivum</i> L.; <i>Stizolobium</i> sp.; <i>Stylosanthes gracilis</i> ; <i>Trifolium repens</i> L.; <i>Vigna catjang</i> V.
Linaceae: <i>Linum usitatissimum</i> L.
Malvaceae: <i>Gossypium hirsutum</i> L.
Mimosaceae: <i>Leucaena leucocephala</i> (Lam.) de Wit.
Musaceae: <i>Musa sapientum</i> M.
Passifloraceae: <i>Passiflora edulis</i> Sims
Pinaceae: <i>Pinus radiata</i> D. Don.; <i>Pinus taeda</i> L.
Poaceae: <i>Avena sativa</i> L.; <i>Digitaria decumbens</i> Stent.; <i>Panicum maximum</i> Jacq.; <i>Pas-</i> <i>palum dilatatum</i> Poir.; <i>Pennisetum clandestinum</i> Chiov.; <i>Saccharum officinarum</i> L.; <i>Sorghum vulgare</i> L.; <i>Triticum aestivum</i> L.; <i>Zea mays</i> L.
Porteaceae: <i>Macadamia integrifolia</i> Maid & Betche
Rosaceae: <i>Fragaria vesca</i> L.; <i>Malus sylvestris</i> Mill.; <i>Prunus domestica</i> L.; <i>P. persica</i> (L.); <i>Pyrus communis</i> L.; <i>Rosa</i> sp.
Rutaceae: <i>Citrus limon</i> (L.) Burm. F.; <i>Citrus paradisi</i> Macfady.; <i>Citrus reticulata</i> Blanco; <i>Citrus sinsensis</i> (L.)
Sapindaceae: <i>Litchi chinensis</i> Sonn.
Solanaceae: <i>Capsicum annum</i> L.; <i>Lycopersicum esculentum</i> Miller; <i>Nicotiana tabacum</i> L.; <i>Solanum tuberosum</i> L.
Vitaceae: <i>Vitis vinifera</i> L.
Zingiberaceae: <i>Zingiber officinale</i> Roscoe.

under 10× magnification. In *H. annuus* L., however, some larvae commenced feeding and formed mines in leaves of the seven replicates (2, 2, and 3 mines respectively). Although some mines reached 10 mm in length, no larvae on *H. annuus* advanced to the next feeding stage of entering and feeding in the stem.

Release in Australia

Approval was received in 1968 from the Commonwealth Department of Health to release *O. balanotes* in Australia. This approval was given with the usual proviso that the insect be reared through one full generation in quarantine facilities to ensure that it was free of parasites and diseases before being released.

Oidaematophorus balanotes was first imported into Australia as larvae in 1969. Small numbers of moths and larvae were released on three

occasions (25 late instars, 20 moths, and 70 first instars, respectively) in southeastern Queensland but establishment was not successful, probably because the numbers released were inadequate.

Further attempts at introduction were made in 1982–83. In autumn 1982 and spring 1983 in Texas, Louisiana, and Florida, larvae were collected by dissecting stems of both *B. halimifolia* and *B. neglecta* at the North American Field Station and placed individually into 2 cm sections of plastic tubing containing Harley-Willson artificial diet (Harley & Willson 1968). A wad of cotton wool acted as a stopper at both ends. In this manner some 500 larvae were shipped to Australia where they were placed on fresh artificial diet to complete their life cycle. However, the larvae responded poorly to this diet and eventually the colony was lost.

A third attempt was made in 1984. Larvae were collected in the summer and autumn of 1984 from Texas and Florida. The finding of a large population of larvae relatively free of parasites near Gainesville, Florida, was an important factor in the ultimate successful colonization of this insect. Approximately 1000 larvae were shipped, mostly from this population at Gainesville, to Australia. This time larvae were reared on potted plants of *B. halimifolia* instead of on artificial diet, using a technique developed by A. J. Tomley at the Alan Fletcher Research Station. The development of this technique was the single most important factor in the success of the program and was the basis for a mass rearing program implemented from 1985–88. Potted plants were exposed to adult moths and plants with eggs were then kept in shade houses until the insect completed its development. As larvae began pupating, their food plants were placed inside temporary cloth cages so that emerging moths could be captured and then released in the field.

Oidaematophorus balanotes reared by this mass production technique were first released in 1985. Over the next 3 years some 10,000 moths were released at various sites in southeast Queensland. Establishment was confirmed in 1985 and the moth is now found throughout most of the range of its foodplant (A. J. Tomley pers. comm.). We anticipate that *O. balanotes* may prove to be one of the better biocontrol agents introduced for this weed (see also Palmer 1989).

DISCUSSION

Oidaematophorus balanotes displays a number of useful characteristics of good biocontrol agents, in addition to its being sufficiently host specific to be used safely in Australia. Its broad native distribution includes a wide range of climatic conditions, including an area with a climate similar to southeast Queensland (Florida), so that its prospects

of successful establishment should have been good. As an endophage, it has a somewhat better chance of success than an ectophage, primarily because endophages are less susceptible to generalist parasitoids and are less likely to be attacked by specialist parasitoids.

A major potential problem of using an insect such as this for biocontrol lies in the difficulty of rearing it in the laboratory. Stem boring insects with relatively long lifecycles can be difficult to rear and the problem is compounded if they do not adapt to artificial diets. Almost certainly the ultimate success of this project was due to the development of suitable mass rearing techniques that produced large numbers of healthy, robust adults available for release.

The successful establishment of *O. balanotes* in Australia provides an example of a problem confronting those involved in biological control. That is, how much effort should be expended on a species when first attempts to establish it fail? Is it better to persevere with such an insect or divert attention to other species? Obviously the answers depend on many factors, but this example suggests that multiple attempts at establishment may be worthwhile.

The effects of *O. balanotes* on *Baccharis halimifolia* in Australia have not yet been ascertained. Populations of the moth, although increasing, have not yet reached damaging levels. Even when the moth is fully established the effects may be difficult to gauge. Unless plants become grossly infested they are unlikely to be killed. Rather, *O. balanotes* may weaken the plants and predispose them to the deleterious effects of other herbivores and pathogens.

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BIOLOGY OF EPIPHYLL FEEDING BUTTERFLIES IN A NIGERIAN COLA FOREST (LYCAENIDAE: LIPTENINAE)

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ABSTRACT. I describe the adult behavior of 16 liptenine butterfly species (Lycaenidae) and include descriptions of oviposition behavior and immatures of 12 from a cola forest near Lagos, Nigeria. Larvae of all species fed on epiphylls such as lichens and fungi, and adults fed at extrafloral nectaries on forest bamboos and vines. I conclude that most species have strictly defensive relationships with ants, the butterfly larvae using their long setae and crevasses in the bark for protection. Larvae of one species (*Aethiopana honorius*) inhabit *Crematogaster* ant runs, and avoid ant attacks by a combination of speed and defensive use of their long lateral setae.

Additional key words: Nigeria, defensive behavior, ants, larval behavior.

No studies of Nigerian Lycaenidae have been published since the classic articles by Farquharson (1921) and Lamborn (1913). These and subsequent works by Jackson (1937), dealing with a wider African fauna, considered mainly those liptenine species associated with ants. Of species not associated with ants, some information is available on two *Telipna* species, one *Mimacraea*, one *Liptena* (Jackson 1937), and two *Pentila* (Clark & Dickson 1971). Here, I report the biology of 12 additional species of Lipteninae, of which 11 are not associated with ants. Notes on adult behavior are included for 16 species. I conclude with a discussion of adult and larval habits.

STUDY AREA AND METHODS

I observed and collected lycaenid butterflies over a two-year period near Lagos, Nigeria. The study area (Fig. 1) was a small forest on the edge of a swamp near Agbara, an industrial estate 40 km west of Lagos. The dominant tree species was *Cola nitida* (Vent.) Schott & Endl., which grows to a height of 10-15 m, forming a closed canopy. Most primary forest in the region has been destroyed, but cola trees are preserved because of the commercial value of their red, pink, and white nuts, which are used locally for chewing and ceremonial purposes. Even so, the cola forest is threatened by the demand for firewood and living space by the nearby urban population. In this surviving cola forest the understory vegetation is usually left to grow along with a few cacao and banana trees that are not sprayed, thus forming a good habitat for many forest species.

I made observations on liptenine biology from July 1986 to March 1988. During the second year I made trips to the study area nearly every weekend, weather permitting, spending a total of 29 days in the field. Initially, I started observations at 0900 h and terminated them at

1600 h. After four months of such long hours, I limited my field time to between 1000 and 1530 h, which I had discovered to include the peak of lycaenid activity. Field observations were recorded on a portable tape recorder and later transcribed to a notebook.

I collected eggs in two ways: by following ovipositing females in the field and by inducing females to lay eggs in captivity. Following females proved unsatisfactory because it required searching the substrata for eggs with a hand lens, by which time the female had usually gone, making identification uncertain. By confining field caught females in plastic bags or wide mouth jars with a piece of moist lichen-covered wood inside, some species could be induced to oviposit. The containers with the females were kept in a naturally ventilated room with no direct light. After hatching, larvae were transferred to jars with fresh epiphyll-covered wood and closed with tissue paper to allow ventilation and prevent mold. High humidity prevented use of totally closed containers, which quickly became moldy, with consequent ill effects for the eggs and larvae.

SPECIES ACCOUNTS

The following 16 liptenine species were recorded at the study site and are listed with observations on their habits and biology.

Ptelina carnuta (Hewitson, 1873)

On numerous occasions I observed adults, both male and female, feeding during the morning hours at extrafloral nectaries of vine tendrils and bamboo, as many as four together and often in the company of other liptenines and ants. When landing, *P. carnuta* held their wings vertically after flexing them a few times.

One female oviposited 5 orange eggs singly on leaf litter on the forest floor at about 1530 h. The female and eggs were taken to the lab, but the eggs never hatched and the female would not oviposit in captivity. Two subsequent attempts to induce other females to oviposit in plastic bags in which dried leaves had been placed also failed.

Pentila nigeriana Stempffer and Bennett, 1961

Adults of both sexes fed on tendril and bamboo nectar between 1000 and 1200 h. Males perched around the trunks of prominent trees on the edge of small openings in the forest between 1100 and 1330 h, which they would circle with a slow, fluttering flight about 4–5 m off the ground before coming to rest on a nearby dry branch. When alighting, they flexed their wings a few times before resting with the wings folded over their backs.



FIGS. 1-6. 1, Cola forest habitat, Agbara, Lagos, Nigeria. The taller trees are *Cola nitida*; 2, *Pentila bitje* ovipositing on a dead branch; 3, *Liptena opaca* feeding on extrafloral nectaries of a creeper; 4, Third instar larva of *Larinopoda aspidos* feeding on epiphylls; 5, Male *Aethiopana honorius* resting on bamboo stem; 6, Larva of *A. honorius*. Note long lateral setae.

A single female oviposited on dried branches near the forest floor at 1340 h. The eggs were laid singly. Brought into the lab, she later placed many reddish-brown eggs on a lichen covered stick in a plastic bag, but the eggs never hatched.

Pentila picena cydaria (Grose-Smith, 1898)

Pentila picena was an avid feeder at bamboo nectaries, with up to 6 individuals of both sexes feeding on the same stem. Male perching habits were similar to *P. nigeriana*, with which *P. picena* shares perching trees. Like *P. nigeriana*, adults of *P. picena* used the tree trunks as reference points, landing on nearby dried branches from which they flew if disturbed, making a few slow circles around the trunk before alighting on the same branch as before and flexing their wings a few times.

I made nine observations of females of this species ovipositing in the forest between 1320 and 1500 h. Eggs were laid singly on live trees and woody stems covered with green lichens and moss. When laid, eggs were white, then became dark brown within a day. In one case two eggs were placed near one another on the same trunk. One female brought into the lab laid numerous eggs on the inside of a glass jar. None of the eggs, either field collected or obtained in the lab, hatched.

Pentila bitje Druce, 1910

The males of this species perched in the company of those of *P. picena* and *P. nigeriana* around the same tree trunk. Flight was slow and fluttery. They alighted invariably on dried branches or tendrils, flexing their wings 3–4 times before closing them over their backs. I observed both sexes feeding on tendril and bamboo extrafloral nectar during the morning (1000 to 1230 h).

On six occasions I observed females ovipositing dark brown eggs (Fig. 2) on dead twigs and branches covered with epiphylls and located near the ground and abandoned termite mounds. Eggs were laid singly between 1300 and 1500 h. Three times I induced females to oviposit in the lab. The larvae hatched in twelve days, refused to eat and died two days later. First instar larvae were light brown with setae longer than the body and extending dorsad and cephalad.

Telipna rothi (Grose-Smith, 1898)

Both sexes fed throughout the morning on bamboo extrafloral nectar. They spent the rest of the day resting in the deeper forest on the undersides of low branches with wings folded. When disturbed, their flight was fairly rapid, similar to that of *Acraea bonasia* Cramer, from which they are indistinguishable on the wing. Upon landing, they did

not flex their wings, their cryptic undersides blending into the background.

One female brought in from the field oviposited brown-gray eggs on dead lichen-covered sticks placed in a plastic bag. The eggs hatched after 10–11 days and the larvae fed on the lichens, spending much of their time in the crevasses or under loose bark. They molted to second instar 9 days later, but refused to eat, despite the introduction of new lichens, and died. Eggs laid by a second female failed to hatch. The head of the second instar was black, thorax and abdomen gray-green with dark lines between the segments, and covered with long setae, the longest dorsad.

Ornipholidotos kirbyi (Aurivillius, 1895)

This species congregated in numbers of up to 6 individuals of both sexes in the morning on vine tendrils and the tips of bamboo shoots where they fed at extrafloral nectaries in the company of ants. When approached by ants, they lowered their wings, keeping them in that position until the ants had retreated. Between 1230 and 1430 h males perched on branches 5–7 m below the forest canopy in groups of up to 4 individuals. Here they chased each other in circles, then landed on branches, and did not flex their wings. Inducing females to oviposit in captivity was unsuccessful.

Mimeresia libentina libentina (Hewitson, [1866])

Both sexes fed between 0900 and 1200 h on bamboo and tendrill extrafloral nectaries. Between 1200 and 1500 h males rested just inside the edge of the woods, hanging from tendrils or dried branches less than 2 m above the ground. Upon landing, they flexed their wings for a minute or two before closing them.

Eresiomera cornesi (Stempffer, 1969)

I observed both sexes feeding on bamboo extrafloral nectaries in the morning. Females appeared to be rare, only two being captured during the two year study period. Between 1200 and 1430 h, males were common at their perching site, which was a large tree trunk around which they chased each other in circles, never lower than 4 m above the ground. To rest, they landed on the tree trunk, flexing their wings a few times.

Citrinophila marginalis Kirby, 1887

Between 0900 and 1600 h, males congregated around the trunks of certain trees, where they rested on nearby leaves 3 to 5 m above the ground. They returned to the same perch after being disturbed, flexing

their wings a few times. Only once did I observe this species feeding on bamboo nectar.

On five occasions I saw females ovipositing in the late afternoon (1400–1500 h). Flying slowly through the undergrowth, females landed on live, smooth-barked trees as well as on dead twigs, upon which they deposited a tiny dark brown egg. Ovipositing females did not flex their wings. Twice females in the lab laid eggs, both times on the sides of the container rather than on the lichen-covered sticks provided. Seven days later the transparent, pubescent larvae hatched, started feeding on the lichen material, and gradually turned the same color as the lichens. However, after the second day of feeding, all larvae stopped eating and died.

Citrinophila erastus erastus (Hewitson, [1866])

Males perched high in the upper story of the forest just below the canopy, 6–7 m above the ground, between 1100 and 1340 h. They rested for long periods on leaf surfaces, flying only when disturbed. Like *C. marginalis*, they flexed their wings a few times upon landing. Lone females were encountered only twice, moving slowly through the undergrowth near the ground in the early afternoon.

Liptena similis (Kirby, 1890)

This species fed on bamboo extrafloral nectaries during the morning (900–1230 h). They congregated in groups of 4–5 individuals of both sexes on a shoot, driving ants away by lowering their wings.

In the laboratory one female oviposited tiny, dark brown eggs with nearly smooth shells. The pubescent brown larvae hatched 13 days later, but refused to eat and died.

Liptena opaca opaca (Kirby, 1890)

In the morning (900–1200 h) this species fed in groups at the nectaries of forest creepers and bamboo shoots in the company of ants and other liptenines (Fig. 3). They lowered their wings to drive away ants. Males chased one another high in the canopy and remained on the wing for long periods, circling in a small area without landing.

I saw one female oviposit on dry branches near the forest floor during the afternoon, but later, in the laboratory, she did not continue ovipositing.

Larinopoda aspidos Druce, 1890

Groups of 5 to 6 individuals of both sexes fed on tendril and bamboo extrafloral nectaries during the morning. Males did not appear to have specific perching sites, but flew in wide, low circles in open areas in

the forest. Adults did not flex their wings when landing, although they lowered their wings to push ants away when feeding. Males have a slightly faster flight than *Pentila*. Females, when searching for oviposition sites, resembled a small white pierid, *Leptosia*, which is very common in the same woods.

I observed 13 ovipositions on dead, epiphyll-covered branches in the woods between 1300 and 1600 h. Females also oviposited readily in the lab. The dark brown eggs hatched within 10 days and the pubescent first instar larvae fed on lichens, seeming to prefer a pale green variety. Molt to the second instar occurred 7 to 9 days later. Individual larvae varied in development time, some molting 3–4 days ahead of their siblings. Second and third instars (Fig. 4) had dark bands on the thoracic and abdominal segments and, on both thorax and abdomen, setae which curve up from the sides and over the back, ending with white bulbous tips, similar to the larvae of *Liptena undina* Smith and Kirby described by Jackson (1937). Molt to the third instar occurred 7 to 10 days later. Larvae crawled under loose pieces of bark, avoiding direct light. They fed almost continuously except the 2 days before molt. Later instars fed on rotten wood as well as on lichen. No larvae survived the third instar.

Tetrarhanis diversa (Bethune-Baker, 1904)

I observed both sexes of this tiny butterfly in the company of other liptenines feeding at tendril and bamboo extrafloral nectaries in the deep forest during the morning.

Twice I found females ovipositing on dead, lichen-covered sticks on the forest floor around 1300 h. After placing a single egg, the female would fly 10 to 20 m before depositing another egg on another stick. None of the three eggs brought into the lab hatched.

Epitola dunia Kirby, 1887

The conspicuous blue males perched during the late morning and early afternoon on the edge of large, sunlit clearings, flying rapidly along the forest margins, then returning to their original perches. They usually rested on dried branches 2–4 m above the ground, their cryptic undersides making them difficult to spot. They did not flex their wings. Females primarily remained deeper in the forest, appearing on the forest margins for mating, where I discovered a copulating pair at 1100 h. I observed one individual of this species being chased and caught by a bird.

I saw a female ovipositing on a dead palm frond at 1315 h. The disk shaped egg hatched 9 days later, but the pubescent larva refused to eat and died after 2 days. Although this genus is reported to be associated

with ants (Lamborn 1913, Jackson 1937), there were no ants where the oviposition was observed.

Aethiopana honorius (Fabricius, 1793)

Males perched in late morning (1100 to 1300 h) on the edge of small sunlit clearings, where half a dozen or more were found together, and not far from the ant trees utilized by their larvae. Males rested by hanging from dead branches or from the bamboo stems from which they fed (Fig. 5). Females frequent the same clearings, but more rarely. Normal flight was rapid and high, the males spectacular as they flashed among the trees. When disturbed while perching, they flew only a short distance before alighting. Their upwing pattern mimics that of distasteful *Bematistes* (Acraeinae).

One female brought into the lab laid a single, disc-shaped egg with serrated edges which did not hatch. Females flew around trees infested with *Crematogaster* ants (Formicidae) and I discovered two larvae moving about the ant runs on the tree trunk near the ant's carton nests. The larvae were dark reddish brown with long lateral setae, and with the body tapering caudad (Fig. 6). Although they normally did not pay attention to the larvae, the *Crematogaster* ants became very aggressive when aroused, as I discovered when I was removing an *A. honorius* larva from the tree. The ants attacked it and were able to get between the setae, causing wounds from which it later died. The second larva was brought into the lab where it fed on lichens for three weeks before dying.

DISCUSSION

Adult Behavior

Liptenine adult behavior is summarized in Table 1. Perching activity by males revealed no marked habitat partitioning in time and space by congeneric species as has been recorded for Neotropical Riodinidae (Callaghan 1983). Most congeneric liptenine species perched in the same localities and over long periods. Perching for most species occurred from slightly before noon until 1400 h, only *C. marginalis* perching earlier in the morning (at 0900 h). Five of 13 species consistently perched near trees, but only one (*cornesi*) actually rested on the tree. Most species landed on dry branches or creepers. In the field, liptenines can be differentiated from butterflies of other families that they mimic, such as Acraeidae, by their resting substrate and behavior. Only the two *Citrinophila* species rested on flat leaves.

Wing flexing upon landing was found only in *Ptelina*, *Mimeresia*, *Pentila*, *Eresiomera*, and *Citrinophila*, all of which share a character-

TABLE 1. Summary of liptenine behavior.

Species	Perching			Wingflex ⁴	Ovipositing	
	Site ¹	Time ²	Substrate ³		Substrate ⁵	Time
<i>P. carnuta</i>	—	—	C	Y	A	1530
<i>P. nigeriana</i>	A	11–1330	A	Y	B	1340
<i>P. picena</i>	A	11–1400	A	Y	C	1320–1500
<i>P. bitje</i>	A	12–1400	A	Y	B	1300–1500
<i>T. rothi</i>	—	—	A	N	B	—
<i>O. kirbyi</i>	B	13–1430	A	N	—	—
<i>M. libentina</i>	C	1030–1400	A	Y	—	—
<i>E. cornesi</i>	A	12–1430	C	Y	—	—
<i>C. marginalis</i>	A	900–1600	B	Y	B, C	14–1500
<i>C. erastus</i>	B	11–1340	B	Y	—	—
<i>L. similis</i>	C	11–1400	A	N	—	—
<i>L. opaca</i>	B	12–1400	A	N	B	1400
<i>L. aspidos</i>	C	11–1300	A	N	B	13–1600
<i>T. diversa</i>	—	—	A	N	B	1300
<i>E. dunia</i>	C	10–1300	A	N	B	1315
<i>A. honorius</i>	C	11–1300	A	N	—	—

¹ Perching Site: A = around a perching tree; B = high above ground, just below canopy; C = woods edge or large sunlit clearings.

² Perching Time indicates the hours of the day during which perching was observed.

³ Perching Substrate: A = tendrils and dry branches; B = leaves; C = tree trunk. For species not observed perching, the substrate used for normal resting is given.

⁴ Wingflex refers to the pumping movement of the wings while the butterfly is at rest: Y = yes; N = no.

⁵ Oviposition Substrate: A = leaf litter; B = dried branches; C = live branches or tree trunks.

⁶ Dash = not observed.

istic slow flight. This behavior may be an advertisement of distastefulness. Despite their slow flight, I never saw birds take any interest in them, although I once observed an *E. cornesi* being stalked by a small lizard. Although the lizard made several attempts to reach the resting butterfly, it was unable to catch it.

Oviposition took place between 1200 and 1600 h for all species observed. Females placed eggs primarily on dry, epiphyll-covered branches near the forest floor, except for *Pentila picena*, which utilized live epiphyll-covered substrates, and *Citrinophila marginalis* and *Larinopoda aspidos*, which used both. *Ptelina carnuta* oviposited on dry leaf litter. All eggs in nature were laid singly and widely spaced, with the exception of one observation of *P. picena*, in which 2 eggs were placed on the same tree trunk.

The major food resource for adult liptenine butterflies was the nectar from extrafloral nectaries. Some forest creepers and bamboos produce from their growing tips a sweet nectar that attracts ants and liptenine butterflies. From morning to early afternoon some creeper and bamboo stems may be visited by numbers of liptenines of different species, which appear not unlike small flags on a pole (Fig. 3). To keep ants away, the butterflies lower their wings and maintain them in that position until the ants have moved away. Whether or not this behavior

has the effect of releasing ant repellent pheromones as suggested by Atsatt (1981) could not be determined.

In wing pattern, *Citrinophila*, *Larinopoda*, and *Liptena* species mimic Pieridae; *Telipna* and *Aethiopana* resemble Acraeinae; and *Telipna* mimic day flying moths.

Behavior of Immatures

Once thought to be rare, the use of epiphylls (liverworts, lichens, bacteria, algae, and fungi) as larval foodplants by butterflies appears to be widespread. Evidence presented here, in addition to that in Jackson (1937), Farquharson (1921), and Clark and Dickson (1971), suggests that this is a major larval food resource for the lycaenid subfamily Lipteninae, currently with 46 genera. In addition, two Satryinae (Singer et al. 1971, DeVries 1986) and one Neotropical genus of Riodinidae, *Sarota* (DeVries 1988, Callaghan unpublished), have been recorded feeding on these food sources. The list probably will grow with future research.

All observations on liptenine larvae were made in the lab from eggs found in the forest and from females induced to oviposit in plastic bags or jars. In the latter case females laid as many as 50 eggs on the sides of the containers or on wood placed inside. However, as all field observations suggested that eggs are laid singly, the number of eggs laid in the lab was presumably a result of the confined environment and stress. Many times the eggs did not hatch, for reasons unknown. In only two cases did larvae pass the first instar and in no case did larvae produce adults. My observations suggest that larval diet is varied, both lichens and rotten wood (fungus?) being consumed by the same species. The food resource of *A. honorius* is the black varnish (fungi/feces?) left by the ants along their runs (Farquharson 1921), although they will feed on epiphylls as well.

One of the major determinants of larval behavior and morphology is their relationship with ants. Among the liptenines I observed, this relationship took two forms; purely defensive, in which the larvae merely protected themselves from aggressive ant behavior (the majority of the species) and opportunistic, in which the larvae took advantage of the ant's aggressiveness for protection against other predators (only in the case of *Aethiopana honorius*).

Cola forests are invaded periodically by driver ants, especially during the rains. Driver ants advance quickly and viciously on a wide front, attacking any creature in their path irrespective of size. Insects and other small animals are immobilized and dismembered in minutes. To test the driver ants' reaction to Lepidoptera larvae, I placed several unidentified pierid larvae among the ants, which immediately attacked

and killed them. The sluggish lichen feeding liptenine larvae would likewise be easy prey, lacking the thick cuticle and ant appeasing nectar glands found in other lycaenids (Atsatt 1981, Cottrell 1984). Also, there is no evidence that liptenines produce pheromones that appease or repel ants. The principal protection for liptenine larvae appears to be their long setae. Once, I observed small red house ants (genus undetermined) enter the *L. aspidos* larva jar and take up residence in the wood. Normally quite aggressive, the ants left the larvae alone after encountering the setae. As larvae spend much time in the crevasses in the bark, the setae apparently form a protective umbrella that prevents ants from getting close enough to bite them. The use of long setae for protection against ants has been suggested by Jackson (1937), Cottrell (1984), and DeVries (1988).

Other liptenine larvae seek protection among ants while not providing any direct benefit to them, such as honeydew secretion. Genera with this behavior are *Aethiopana*, *Hewitsonia*, *Tetartoneura* (Farquharson 1921, Jackson 1937, my own observations in Zaire) and *Epitola* (Jackson 1937), although in the case of the latter my observation of oviposition far from the ant runs may suggest both purely defensive and opportunistic behavior for that genus.

Aethiopana honorius larvae evidently avoid predation by inhabiting ant runs, which are hostile environments for many potential predators. Other Lepidoptera larvae without long hairs and other insects that I placed in the ant runs were immediately attacked. Although the ants do not normally bother *honorius* larvae, they will attack if excited and will bite the larvae if they can get between or under their setae, as related earlier. Farquharson (1921) described a similar experience in which larvae in a jar were attacked by ants. Larvae of *A. honorius* are protected by their long setae and by moving about the ant runs on their long legs at a speed equal to that of the ants themselves. When the ants become excited, the larvae beat a hasty retreat, flicking the last abdominal segments to shake off any attacking ants that may have become lodged among their setae. Similar behavior occurs among *Hewitsonia* larvae in Zaire (Callaghan unpublished), suggesting an exception to the assertion by Cottrell (1984) and Atsatt (1981) that lycaenid larvae lack a "thrashing reflex" found in other lepidopterous larvae, presumably because rapid movements incite ant aggression. The rapid movement of *A. honorius* and *Hewitsonia* transports them out of danger by not allowing excited ants the chance to gang up on them; the flicking removes ants entangled in the setae. Such behavior also works because the larvae remain in the runs where ants are not densely packed, category L2 of Cottrell (1984). The larvae will not enter the ants' carton nests. I tried pushing a *Hewitsonia* larva towards the nest, but it kept

trying to move in the opposite direction. There is nothing in the behavior of larvae of either species that would suggest that they use ant appeasing pheromones.

Finally, in addition to living in the ant runs, larvae with long setae gain additional protection from vertebrate predation by mimicking larvae of moths of the family Lymantriidae, which also inhabit the same ant runs and have tufts of stinging dorsal spines.

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POTENTIAL FOR THE NON-INVASIVE STUDY OF INSECT HEART FUNCTION WITH A DOPPLER CRYSTAL SYSTEM

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ABSTRACT. This report describes a new technique for the non-invasive physiologic study of butterfly and moth circulatory systems. The technique employs a miniature Doppler crystal for *in vivo* assessment of circulatory function and provides information not obtained by previously reported methods.

Additional key words: blood flow, velocimeter, dorsal vessel, aorta, cardiac output.

The insect circulatory system has been studied extensively with reviews of structure and function (Davey 1964, Jones 1973, 1977, McCann 1970, Wigglesworth 1971). Although limited visual and photoelectric recordings of the insect heartbeat have been reported (Jones 1973, Tachibana & Nagashima 1957), most studies of *in vivo* function have required invasive electrical techniques (Miller 1973). Advances in miniature Doppler technology in the study of the human cardiovascular system can be applied to the study of insects. This report describes a new technique for the non-invasive evaluation of butterfly and moth circulatory systems.

METHODS

A 20 MHz Doppler catheter Model DC-201 (Millar Instruments, Inc., 6001-A Gulf Freeway, Houston, Texas 77223-0227) was used for transmitting and receiving acoustic signals. This catheter consists of a 20 MHz circular ceramic crystal attached to the tip of a USCI Rentrop Reperfusion Catheter, 135 cm length tapering to 1 mm diameter tip (Millar Instruments). This catheter is used for intravascular measurement of blood flow in the human coronary artery (Sibley et al. 1986). Two wires attached to the crystal traverse the lining of the catheter and are connected to a range-gated 20 MHz pulsed Doppler velocimeter (Millar Instruments) that detects the Doppler shift of the echoes from the blood cells. The velocimeter transmits pulses of 20 MHz ultrasound from the crystal at the catheter tip into the dorsal vessel. During the pause between pulses the crystal serves as a sensor and receives echoes from the blood cells. The distance between the crystal and the echo source may be varied from 1 to 10 mm by the range control on the velocimeter. The polarity of the phase shift (plus or minus 90 degrees) is determined by the direction of the motion either toward or away from the Doppler crystal. The pulsed Doppler velocimeter provides an audio signal with phasic output display. This phasic velocity signal from the pulsed Doppler velocimeter is recorded on a strip chart recorder

(Meda Sonics Model R 12 B, 340 Pioneer Way, Box 7268, Mountain View, California 94039). The strip chart recording displays not only the rate but the wave form of the Doppler shift frequency change at a specific distance from the transducer. Since the Doppler shift frequency is directly proportional to the velocity of the flow, the peak velocity can be measured at the peak of the wave form above the zero line (Hartley & Cole 1974). Audio recording was accomplished with a standard cassette tape recorder. The velocimeter was calibrated following the steps of the manufacturer (Millar Instruments).

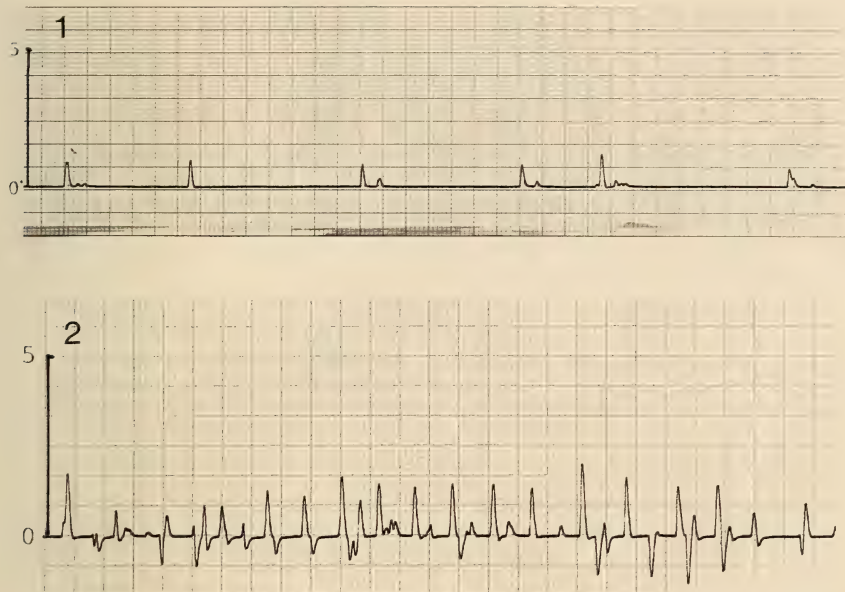
The butterfly or moth was placed on a standard mounting board where it was carefully positioned with wings spread and held down by paper strips. The body rested in the open midline groove but was not penetrated by pins. The tip of the Doppler catheter was then held over the dorsal midline upper abdomen or thorax lightly touching the insect. Conduction of the Doppler signal was enhanced by the use of a small amount of ultrasound transmission gel (Aquasonic 100—Parker Laboratories, Inc., Orange, New Jersey 07050) between the tip of the catheter and the body of the insect. The range control on the Doppler velocimeter was adjusted from 1 to 10 mm for sampling. Audio volume (loud, high signal to noise ratio) was used to guide the optimal sampling depth and angle of the catheter tip over the dorsal vessel with respect to the body of the insect.

RESULTS

Audible signals were recorded from the following species: *Epargyreus clarus* Cramer (Hesperiidae), *Limenitis arthemis* (Drury) (Nymphalidae), *Danaus plexippus* Linnaeus (Nymphalidae) over the thorax (aorta and/or pulsatile organ); and the moth *Catocala judith* Strecker (Noctuidae) over the upper abdomen (heart). At room temperature (22°C) heart rhythm was irregular in all species. The rate was variable at rest from as low as 20 to 30 per minute in *C. judith* (Fig. 1), to over 210 per minute in *E. clarus* (Fig. 2). The maximum peak velocity recorded was 2.0 cm/sec in *E. clarus*, 1.3 cm/sec in *L. arthemis*, and 1.5 cm/sec in *C. judith*. Because heart rate is variable, variations in peak velocity are expected. This variation was apparent at rapid rates (shortened diastole may impair adequate filling), but also occurred even at slower rates when filling should not be impaired. Reverse flow was noted by the negative deflection (below baseline) of the phasic wave form, generally following the positive flow wave (Fig. 2).

DISCUSSION

This report describes a new technique for the study of the butterfly and moth circulatory system. The technique potentially could be ap-



FIGS. 1 and 2. **1**, Doppler recording of *C. judith* heart activity. The maximum flow velocity for each heartbeat is the peak of the vertical distance (cm/sec) from the zero line. The paper speed is 25 mm/sec on the horizontal scale. The peak flow velocity on this recording is 1.2 m/sec; **2**, Doppler recording of *E. clarus* heart activity. The rate is rapid and the rhythm is irregular with variable peak velocities (cm/sec on the vertical scale). The deflections below the zero baseline indicate reverse flow. Paper speed on the horizontal scale is 25 mm/sec.

plied to other insects whose dorsal vessel is of sufficient size (minimal diameter unknown) to be within the resolution of the Doppler crystal frequency. The non-invasive feature of this technique minimizes trauma to the insect. Thus, multiple observations over time in the same subject may be performed. This technique avoids the artifactual changes that may be introduced with invasive *in vivo* techniques. Furthermore, the Doppler technique provides *in vivo* flow information not obtained by any other previously described method of study of the insect circulatory system. Using this technique, heart rate and flow parameters in the same subject could be obtained under varying conditions, or the rate and flow variables in different subjects could be compared under similar conditions. In addition, the flow per unit time can be calculated as the sum of the areas under the curves per unit of time (Cole & Hartley 1977, Perez 1987). Thus, if the radius of the vessel is known at the sample location, cardiac output (ml/min) can be calculated (Haites et al. 1985). Calculation of the forward cardiac output would require subtraction of the reverse flow per unit time.

Reviews of electrical and optical methods for recording the insect heartbeat are reported elsewhere (Jones 1977, Miller 1973). The variable heart rates of the Lepidoptera in this study are similar to those previously reported, but audio recordings have not been described.

Earlier studies of dorsal vessel muscle contraction reviewed elsewhere (Beard 1953, Miller 1985) have involved visual and invasive mechanical devices to study the peristaltic wave contraction. There are no previous studies of blood flow velocity in the dorsal vessel. This technique provides such information non-invasively.

Heartbeat reversal in which peristaltic waves of contraction are directed from front to back (reverse or retrograde peristalsis) are well described in insects since the first visual observation by Malpighia in 1669 (Gerould 1929, Davis 1961). This phenomenon has been attributed to changes in automaticity in cardiac pacemakers anteriorly and posteriorly, spontaneously or secondary to various stimuli (Davis 1961). Characteristically, anterograde (traveling anteriorly) peristaltic contractions occur for a period of beats then reverse or retrograde peristalsis occurs. This heartbeat reversal is to be distinguished from the reverse or backward blood flow pattern seen in the present study, usually immediately following the forward flow. This brief reverse flow is likely secondary to the characteristics of the open-end circulatory system. The hemolymph of insects is aspirated into the heart during diastole under a negative pressure (Wigglesworth 1971). Since the dorsal vessel is open-ended and without intraluminal valve structures to prevent back flow, some reverse flow is expected. Elastic recoil of the vessel wall and supporting structures may accentuate this effect (increased vascular compliance). However, this explanation cannot be proved without simultaneous Doppler flow pattern and electrical or visual observation of the peristaltic wave form.

The disadvantages of this technique include the immobilization of the insect, thus limiting conditions of the physiologic assessment. In addition, electrical artifact on the chart recorder at times limited the ability to record on paper the Doppler signal though it was easily audible. The etiology of the artifact is uncertain but likely is secondary to limitations of the strip chart recorder. A strip chart recorder with bioelectric amplifiers may reduce or eliminate this problem. Noise artifact may be produced by movement of the catheter tip on the insect body but this was not a significant problem. Occasional wing muscle contraction introduced noise artifact, most prominent in *E. clarus*, but this was usually brief and did not interfere with recordings. Gut movement did not produce noticeable noise artifact. Auditory artifact from electrical interference and its elimination from the velocimeter is detailed by the manufacturer (Millar Instruments). There was some dif-

difficulty in holding and positioning the catheter tip, especially for prolonged measurements. Measured flow rates may be underestimated by this technique with improper angulation between the transducer crystal and the vessel flow (Perez 1987).

Refinements and improvements in instrumentation specifically directed toward the study of the insect circulatory system should reduce these drawbacks. This technique offers an important new method for the non-invasive *in vivo* physiologic assessment of the butterfly and moth circulatory systems, and potentially other insects.

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TWO NEW SPECIES OF MOTHS
(NOCTUIDAE: ACRONICTINAE, CUCULLIINAE)
FROM MIDLAND UNITED STATES

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ABSTRACT. Two new species of noctuid moths are described and illustrated. *Acronicta heitzmani*, new species, in the subfamily Acronictinae, is known from Missouri, Arkansas, Illinois and Ohio. *Lithophane joannis*, new species, in the subfamily Cuculliinae, is known from Ohio, Kentucky, and Michigan. Both species are compared with morphologically similar congeners.

Additional key words: *Acronicta heitzmani*, *Lithophane joannis*, faunal survey.

Since their origins, the Ohio Lepidopterists and the Society of Kentucky Lepidopterists have promoted regional surveys of the Lepidoptera fauna of midland United States. These efforts have resulted in numerous new records and range extensions and in the discovery of several new taxa. The purpose of this paper is to describe and illustrate two recently discovered species of the family Noctuidae. Both apparently are restricted to midland United States. *Acronicta heitzmani*, new species, is known from Missouri, Arkansas, Illinois and Ohio. *Lithophane joannis*, new species, is known from Ohio, Kentucky, and Michigan. Both species are morphologically distinct from, and sympatric with, congeners.

In 1964, J. R. Heitzman collected a series of an unusual *Acronicta* species in Missouri. The specimens superficially resembled *A. fragilis* (Guenée) which was not recorded from Missouri. In 1967, the first author collected a specimen of the same species in Kentucky; the second author took the first Ohio specimen in 1975. The specimens were determined as a possibly undescribed species near *A. fragilis* by the late E. L. Todd of the Systematic Entomology Laboratory, U.S. Department of Agriculture. In 1986 J. D. Hooper collected typical *A. fragilis* together with the new species in Shawnee State Forest, Scioto Co., Ohio; more recently, both were collected together at Tunnel Ridge, Red River Gorge, Powell Co., Kentucky, by L. D. Gibson. Over the years, collections of this species have resulted in a study series of 92 specimens from 5 states. Characteristics that distinguish this species are remarkably constant throughout its range. We therefore describe this insect as a new species.

The new species of *Lithophane* was collected in Ohio in 1975 by the second author, who recognized it as an undescribed species on the basis of male genitalic characters. More specimens were recorded from Ohio and Kentucky in the 1980's. In 1990 M. C. Nielsen took two specimens in Lenawee Co., Michigan. We initially assumed that this species had remained undescribed because of its close resemblance to "ferralis" phases of *Lithophane petulca* Grote and *L. hemina* Grote; however, only two specimens that predate 1975 were located in any collection.

No specimens of either of the new species were found in the American Museum of Natural History, Carnegie Museum of Natural History, Canadian National Collection, Field Museum of Natural History, Illinois Natural History Survey, Ohio State University collection of insects, Michigan State University Department of Entomology, or University of Michigan.

***Acronicta heitzmani* Covell and Metzler,**

new species

(Figs. 1, 2, 7, 8, 9)

Diagnosis. *Acronicta heitzmani* is similar to *A. fragilis* in forewing pattern (see Figs. 1–4), but it is slightly smaller—individuals range 1.0–1.5 mm shorter in forewing length. Black areas of the forewing in *A. fragilis* are replaced by olive gray in *A. heitzmani*, giving it a more uniform olive gray ground color. The scaling between the double antemedial and postmedial lines and in the suborbicular spot are gray in *A. heitzmani* rather than white as in *A. fragilis*. The hindwing is gray in *A. heitzmani*, not white with gray shading as in *A. fragilis*. The male valvae are slightly longer in relation to their width in *A. heitzmani* (see Figs. 6 and 7).

Description (Figs. 1 and 2). Head with frons usually more outwardly bulging than in *A. fragilis*. Vestiture of body similar to *A. fragilis*, but abdomen darker grayish. Forewing length 12.0–14.5 mm ($n = 67$) in males, 12.5–15.0 mm ($n = 25$) in females. Forewing above olive gray with black lines and spots contrasting less than in *A. fragilis*, which is black and whitish; lower half of postmedial line less deeply incurved than in *A. fragilis*. Filling of postmedial line, subterminal shade, and terminal line whitish. Fringe checkered olive-gray and white. Hindwing above dull gray; discal dot and median line faintly expressed. Terminal line broken, thin, blackish, with fringe as in forewing. Both wings shiny gray below, forewing darker. Lines of upperside faintly repeated beneath, darkest at costa; terminal lines of fine black dots. Color and pattern similar in both sexes and uniform among specimens studied.

Male genitalia (Fig. 7). Similar to that of *A. fragilis* (Fig. 6), but valva longer in relation to width, and not narrowing noticeably beyond valvula. Ampulla wider and shorter than that of *A. fragilis*. Aedeagus much smaller—nearly half the size of that in *A. fragilis*.

Female genitalia (Fig. 8). No consistent differences between those of *A. heitzmani* and *A. fragilis* are apparent. As with adults in general, the genitalia of *A. heitzmani* are smaller than those of *A. fragilis*.

Types. Holotype, male: Missouri, Benton County, Harry S. Truman State Park, near Warsaw, 24 July 1965, at blacklight, J. R. Heitzman. Paratypes, 66 ♂♂ and 25 ♀♀, as follows:



FIGS. 1-5. *Acronicta* and *Lithophane* species. 1, *Acronicta heitzmani*, holotype male. 2, *Acronicta heitzmani*, paratype female, Boone Co., Kentucky, 18 May 1980, L. D. Gibson. 3, *Acronicta fragilis*, male, Harlan Co., Kentucky, 14 July 1979, C. V. Covell Jr. 4, *Acronicta fragilis*, female, Powell Co., Kentucky, 21 May 1988, C. V. Covell Jr. 5, *Lithophane joannis*, holotype male.

ARKANSAS: Madison Co.: Blue Springs State Park, east of Springdale, 15 April 1967 (1 ♂), R. L. Heitzman. Washington Co.: Devil's Den State Park, 22 July 1967 (1 ♂, 1 ♀), R. W. Hodges. MISSOURI: Benton Co.: same locality as holotype, 26 July 1964 (3 ♂♂), 7 May 1965 (1 ♀), 24 July 1965 (1 ♂), 8 August 1965 (1 ♂), 7 August 1966 (2 ♂♂), 27 July 1967 (2 ♂♂, 1 ♀), 15 May 1969 (1 ♂), 7 May 1970 (1 ♂, 3 ♀♀), 5 August 1971 (1 ♂), all R. L. Heitzman. Boone Co.: Ashland Wildlife Area, deciduous forest, 12 April 1977 (1 ♂), 14 April 1977 (1 ♂), 21 April 1977 (2 ♂♂), all R. L. Heitzman. Grundy Co.: Crowder State Park, marsh and deciduous forest, near Trenton, 21 July 1979 (1 ♂), 24 May 1980 (1 ♀), R. L. Heitzman. Jefferson Co.: Victoria Glade, 4 km (2.5 miles) SE Hillsboro, 24 April 1982 (4 ♂♂), George Balogh. Laclede Co.: 3 km (2 miles) SE Stoutville, 2 August 1975 (4

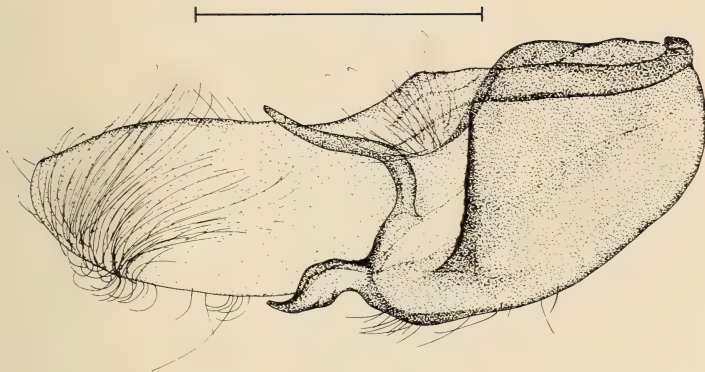


FIG. 6. *Acronicta fragilis*. Male genitalia left valve. Slide C.V.C.Jr. 1186. Bell Co., Kentucky, 3 May 1974, Carl C. Cornett. Scale bar = 1 mm.

♂♂, 1 ♀), 10 April 1976 (2 ♂♂), 31 July 1976 (6 ♂♂, 2 ♀♀), R. L. Heitzman. Ste. Genevieve Co.: Hawn State Park, 10 April 1981 (1 ♂), 27 July 1984 (1 ♂), T. C. Macrae. ILLINOIS: McDunnough Co.: Macomb, 22 April 1985 (1 ♂), Y. Sedman. KENTUCKY: Boone Co.: Big Bone Lick State Park, 2 May 1979 (3 ♂♂, 3 ♀♀), 19 May 1979 (1 ♀), 5 May 1980 (1 ♂, 1 ♀), 18 May 1980 (1 ♂, 5 ♀♀), L. D. Gibson; Camp Earnst, 17 August 1979 (1 ♂), L. D. Gibson. Jefferson Co.: Valley Station, 3 May 1987 (1 ♂), B. S. Nichols. Meade Co.: Fort Knox, 9 August 1975 (1 ♂), S. Sholz; Otter Creek Park, 10 May 1987 (1 ♀), B. S. Nichols. Oldham Co.: Horner Wildlife Sanctuary, 14 August 1967 (1 ♀), C. V. Covell Jr. Powell Co.: Tunnel Ridge, 14 May 1988 (1 ♂), 3 May 1991 (1 ♂), L. D. Gibson. OHIO: Adams Co.: Green Township, Waggoner Riffle Rd. at Black Run Rd., 1 August 1981 (2 ♂♂), E. H. Metzler. Scioto Co.: Shawnee State Forest, clearcut on state forest Rt. 2, ca. 0.6 mile east of state forest road 13, 16 July 1986 (4 ♂♂); clearcut 1 mile south of Pond Run Tower, 18 July 1986 (8 ♂♂), 20 August 1986 (1 ♂), J. D. Hooper. Vinton Co.: Richland Township, Section 24, 1 August 1975 (1 ♂), 30 July 1976 (1 ♂), 28 May 1978 (1 ♀), 24 May 1981 (1 ♂, 1 ♀), and 15 May 1982 (1 ♀), E. H. Metzler.

Disposition of types. Holotype and paratypes in the National Museum of Natural History, Washington, D.C.; paratypes at American Museum of Natural History, New York; California Academy of Sciences, San Francisco, California; Canadian National Collection, Ottawa, Ontario; Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; Field Museum of Natural History, Chicago, Illinois; Florida State Collection of Arthropods, Gainesville, Florida; Los Angeles County Museum of Natural History, Los Angeles, California; Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; The Natural History Museum, London, England; University of Louisville, Louisville, Kentucky; and private collections of George J. Balogh, Portage, Michigan; Loran D. Gibson, Florence, Kentucky; J. Richard Heitzman, Independence, Missouri; Jeffrey D. Hooper, Uniontown, Ohio; Eric H. Metzler, Columbus, Ohio; Barry S. Nichols, Louisville, Kentucky; and Yale Sedman, Macomb, Illinois.

Type locality. Described by J. R. Heitzman (pers. comm.) as oak-hickory forest interspersed with cedar glades. Understory trees, shrubs, and vines include *Bumelia* (Sapotaceae), *Celtis* (Ulmaceae), *Cercis* (Fabaceae), *Crataegus* (Rosaceae), *Gleditsia* (Fabaceae), *Gymnocladus* (Fabaceae), *Prunus* (Rosaceae), *Viburnum* (Caprifoliaceae), *Sassafras* (Lauraceae), *Zanthoxylum* (Rutaceae), *Ceanothus* (Rhamnaceae), *Ribes* (Saxifragaceae), *Rhus* (Anacardiaceae), *Vaccinium* (Ericaceae), *Aristolochia* (Aristolochiaceae), *Smilax* (Liliaceae), and *Vitis* (Vitaceae). Elevation is approximately 260 meters.

Immature stages. Unknown. One female produced 3 ova in captivity but the larvae refused to eat alder, *Alnus serrulata* (Ait.) Willd. (Betulaceae), and river birch, *Betula nigra* L. (Betulaceae).

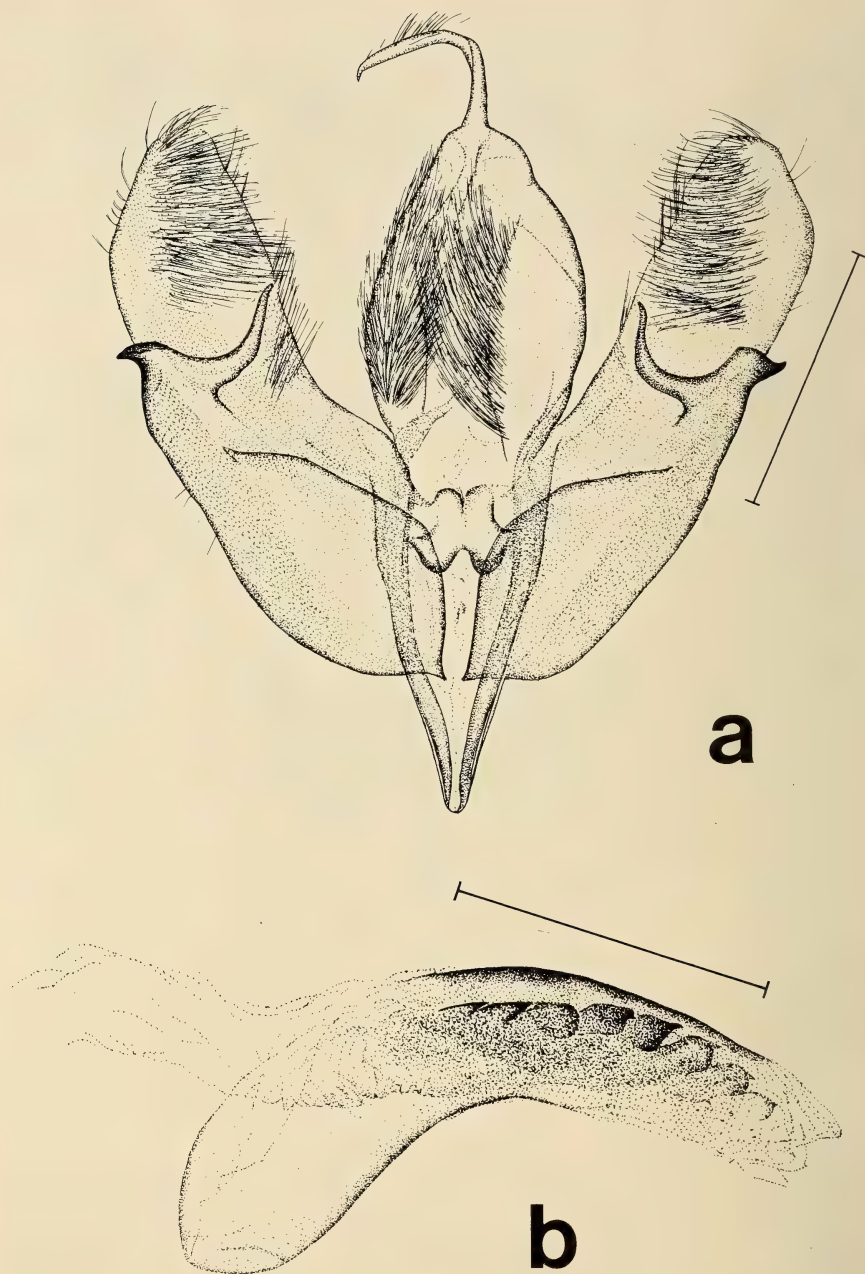


FIG. 7. Male genitalia of *Acronicta heitzmani*. a) Genitalia with aedeagus removed; b) Aedeagus. Slide C.V.C.Jr. 1172. Paratype, Adams Co., Ohio, 1 August 1981, E. H. Metzler. Scale bar = 1 mm.



FIG. 8. Female genitalia of *Acronicta heitzmani*. Slide C.V.C.Jr. 1185. Paratype, Oldham Co., Kentucky, 14 August 1967, C. V. Covell Jr. Scale bar = 1 mm.

Geographical distribution. Southeastern Ohio to Illinois, Missouri, and northern Arkansas (Fig. 9).

Flight period. Two broods, April through early June, and mid-July to late August.

Discussion. The known range of *Acronicta fragilis* extends from Newfoundland to Florida, west across Canada, and south to Kentucky (Covell 1984:85). The known range of *A. heitzmani* lies within the

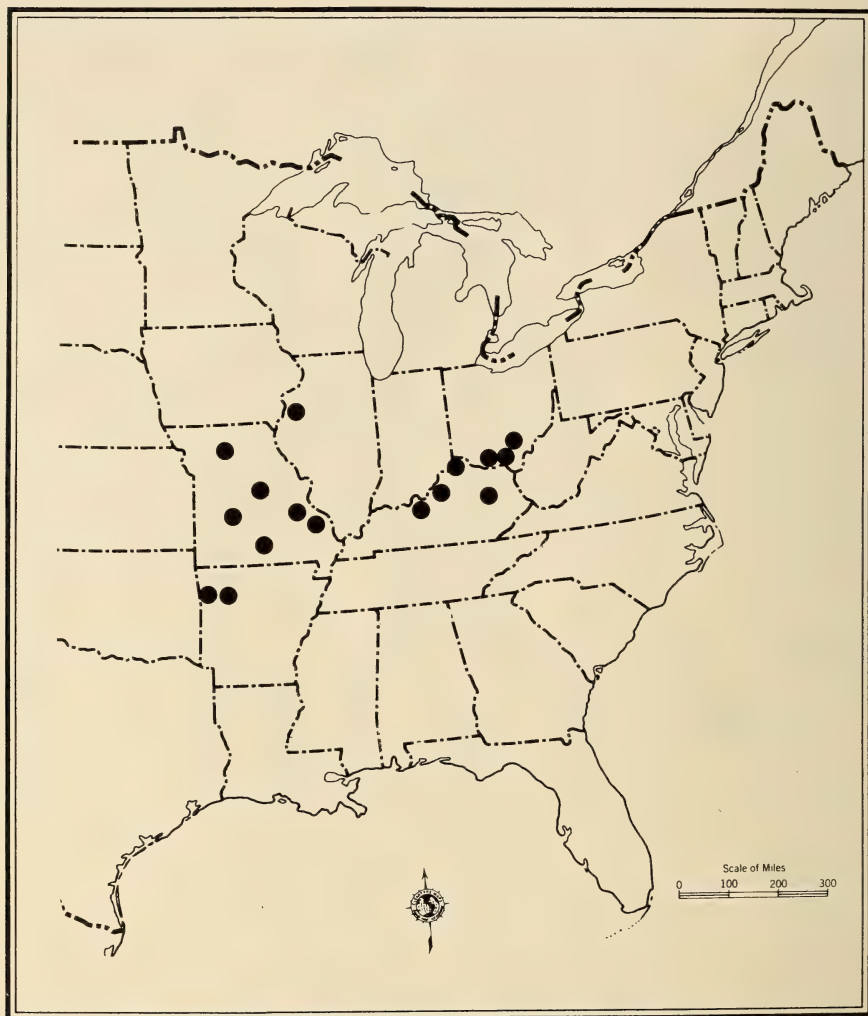


FIG. 9. Geographical range of *Acronicta heitzmani* in the United States.

southern part of the range of *A. fragilis*, west of the Appalachian Mountains. It also extends farther to the southwest than *A. fragilis*, reaching northern Arkansas. Heitzman (pers. comm.) has not found *A. fragilis* in Missouri or Arkansas.

Etymology. The authors take pleasure in naming this species in honor of J. Richard Heitzman, who collected the first known specimens and who has made many significant contributions to North American lepidopterology.

***Lithophane joannis* Metzler and Covell,
new species**

(Figs. 5, 10, 11, 12)

Diagnosis. *Lithophane joannis* is similar to “ferrealis” phases of *L. hemina* and *L. petulca*, and the typical form of *L. oriunda* Grote (Noctuidae). It can be separated from *L. oriunda* by its darker black-brown color and less contrasting pale outlines of the orbicular and reniform spots, and from *L. hemina* and *L. petulca* by the more evenly excurved terminal line. The costal area is not as pale as the “lignicosta” form of *L. hemina*, and lacks the bluish cast of the “ferrealis” form of *L. petulca* (Franclemont 1942). The forewing has neither contrastingly pale scales outlining the claviform spot nor very dark scales in medial area of the fold often found on *L. hemina* form “lignicosta.”

Description (Fig. 5). Dorsal thorax dark brown with pale mid-thoracic crest between collar and abdomen. Legs, palpi, head, and collar pale. Front crossed laterally by a black line. Abdomen brown with five obscure dorsal tufts. Forewing length 15.0–17.0 (n = 82) in males and females. Forewing above umber and black-brown. Pale reddish brown costa continues to basal dash; the latter defined by pale. Orbicular spot pale, flattened laterally. Reniform spot dark with pale outline, often smudged with pale scales. Orbicular and reniform spots with filling slightly paler than dark ground color. Antemedial line obscure, single, deeply zigzagged basally on veins and distally between veins, doubled through the pale costa; marked with three pale dots at the radial, medial, cubital, and anal veins. Similar postmedial line zigzags distally on veins, basally between veins; marked by six obscure pale dots at the radial, medial, cubital, and anal veins. Medial line marked only by a dark shade at the costa. Two terminal lines: one pale, excurved, nearly parallel to the outer margin; the other fine, black; base of fringes pale. Subterminal area darker on paler specimens. Hindwing above dark fuscous with darker veins; a dark discal lunule and dark terminal line. Fringe tips pale. Forewing below uniformly dark fuscous with costa and terminal area slightly paler. Costa just before terminal area marked with four dark and three pale shades; reniform spot of dark shade. Hindwing below paler than forewing, dusted with dark scales; marked by dark postmedial line, dark discal spot, and dark terminal line. Fringes pale. Males and females similar in color and pattern. Spring specimens range from black-brown to faded umber brown, never pale.

Male genitalia (Fig. 10). Similar to *L. oriunda*, *L. hemina*, and *L. petulca*, but the base of the valve with a prominent dorsal lobe not found in those species. At the narrowest point, the central ridge of the juxta is at least $\frac{1}{2}$ wider than in the other three species.

Female genitalia (Fig. 11). The ductus bursae is 45% shorter than that in *L. hemina* and *L. petulca*.

Types. Holotype male: Ohio, Greene County, John Bryan State Park, 30 October 1989, E. H. Metzler. Paratypes, 40 ♂♂ and 39 ♀♀, as follows: KENTUCKY: Boone Co: Big Bone Lick State Park, 20 February 1986 (1 ♂, 2 ♀♀), 25 March 1986 (1 ♂, 1 ♀), both D. J. Wright, 20 March 1979 (1 ♀), 23 March 1980 (1 ♀), 25 March 1986 (2 ♀♀), all L. D. Gibson; Boone Cliffs Nature Preserve, 17 March 1982 (3 ♂♂, 2 ♀♀), 24 March 1982 (1 ♀), both L. D. Gibson. Carroll Co: General Butler State Park, 29 March 1980 (2 ♂♂, 3 ♀♀), L. D. Gibson. Jefferson Co: Camp Cedar Ridge, 15 February 1981 (1 ♀), R. A. Henderson; Louisville, 9 March 1977 (1 ♂, 2 ♀♀), C. V. Covell Jr. Menifee Co: north of Slade Road, vicinity Red River, Edward Branch, elev. 900 ft, 3–8 March 1980 (1 ♂), J. S. Nordin. Meade Co: Otter Creek Park, 17 March 1979 (1 ♀), R. A. Henderson. MICHIGAN: Lenawee Co: T8S, R2E, Section 31, 21 March 1990 (1 ♂, 1 ♀), M. C. Nielsen. OHIO: Adams Co: 1 mi [1.3 km] SE Lynx, P. Knoop Property, 20 March 1991 (1 ♀), L. D. Gibson. Delaware Co: Alum Creek State Park, 15 March 1977 (1 ♂), E. H. Metzler. Fairfield Co: Wahkeena Nature Preserve, Berne Township, Section 4, 11 March 1977 (1 ♂), E. H. Metzler (EHM slide no. 100). Franklin

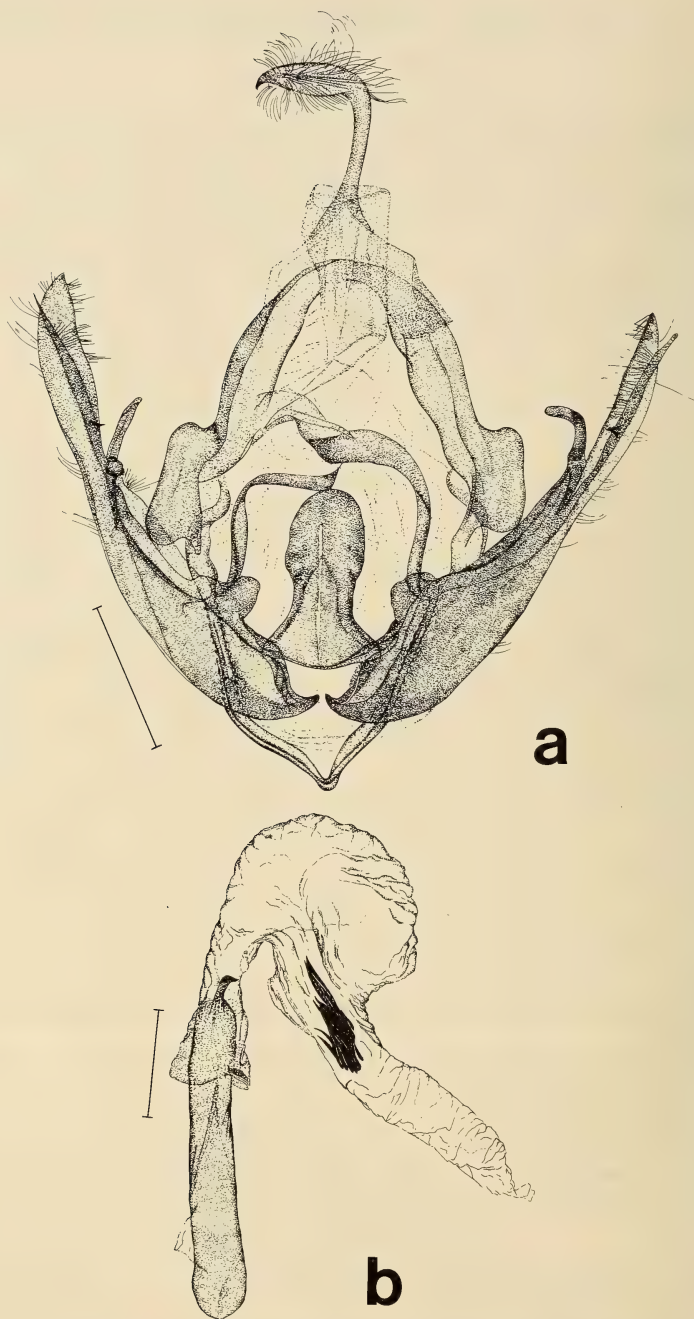


FIG. 10. Male genitalia of *Lithophane joannis*. a) Genitalia with aedeagus removed; b) Aedeagus. Slide E.H.M. 110. Paratype, Greene Co., Ohio, 10 March 1990, E. H. Metzler. Scale bar = 1 mm.

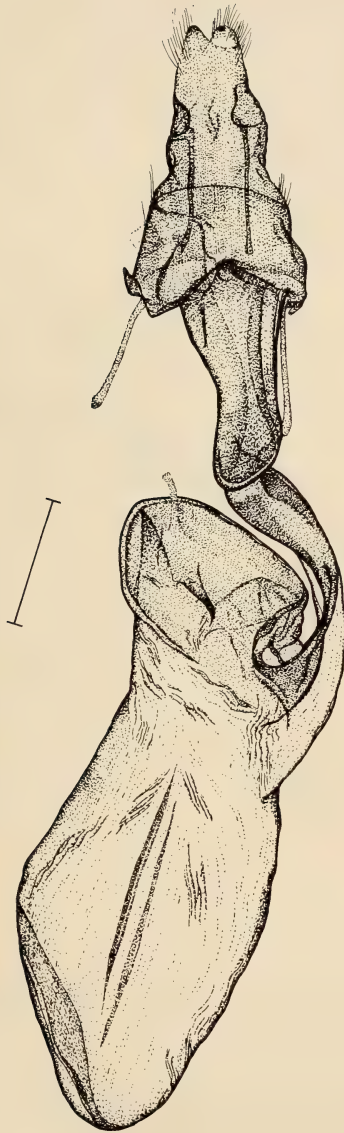


FIG. 11. Female genitalia of *Lithophane joannis*. Slide E.H.M. 111. Paratype, Fulton Co., Ohio, 10 March 1989, R. W. Rings. Scale bar = 1 mm.

Co: Blendon Township, Hoover Dam, 22 February 1975 (1 ♀), E. H. Metzler; Jefferson Township, Gahanna Woods Nature Preserve, 19 March 1976 (1 ♂), E. H. Metzler. Fulton Co: German Township, Goll Woods, 11 March 1989 (1 ♀), R. W. Rings (EHM slide no. 111). Greene Co: John Bryan State Park, 14 March 1989 (3 ♂♂) (EHM slide nos. 112, 113), 16 April 1989 (2 ♀♀) (EHM slide nos. 114, 115), R. W. Rings, 30 October 1989 (2 ♀♀), 10



FIG. 12. Geographical range of *Lithophane joannis* in the United States.

March 1990 (12 ♂♂, 5 ♀♀) EHM slide nos. 110, 116), 16 April 1990 (1 ♀), 3 March 1992 (5 ♂♂, 7 ♀♀), E. H. Metzler. Hamilton Co: Cincinnati, 9 March 1986 (1 ♀), 13 March 1986 (2 ♂♂, 1 ♀), D. J. Wright. Lawrence Co: Lake Vesuvius, 10 October 1984 (1 ♂), R. W. Rings. Vinton Co: Richland Township, Section 24, 3 March 1979 (1 ♂), E. H. Metzler. Wayne Co: Wooster, 4 March 1970 (1 ♂), R. W. Rings. No county: Skinner collection [no date] (1 ♂).

Disposition of types. Holotype and paratypes in the National Museum of Natural History, Washington, D.C.; paratypes in Academy of Natural Sciences, Philadelphia, Pennsylvania; American Museum of Natural History, New York; Canadian National Collection, Ottawa, Ontario; Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; Florida State Collection of Arthropods, Gainesville, Florida; Los Angeles County Museum of Natural History, Los Angeles, California; Michigan State University, De-

partment of Entomology, East Lansing, Michigan; Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; The Natural History Museum, London, England; Ohio State University, Ohio Agricultural Research and Development Center, Wooster, Ohio; University of Louisville, Louisville, Kentucky; Ohio Lepidopterists' collection, Ohio State University, Columbus, Ohio; and private collections of John G. Franclemont, Department of Entomology, Cornell University, Ithaca, New York; Loran D. Gibson, Florence, Kentucky; Eric. H. Metzler, Columbus, Ohio; Mogens C. Nielsen, Lansing, Michigan; and Donald J. Wright, Cincinnati, Ohio.

Type locality. The type locality is a mature, second growth, mixed mesophytic hardwood forest along a ridge trail overlooking the Little Miami River at the campground in John Bryan State Park. The exact location where the holotype was collected is 39°47'04"N, 83°51'57"W.

Immature stages. Unknown. One female produced 17 ova in captivity but the larvae refused to eat a variety of woody plants that were offered.

Geographical distribution. Southeast Michigan, Ohio, and north-central Kentucky (Fig. 12).

Flight period. October through April.

Discussion. *Lithophane joannis* probably has gone undetected because of its limited geographic range coupled with a dearth of collecting efforts for "winter moths" as described by Newman (1945). Only two specimens that predate 1975 were located in any collection; most collections have no specimens. This species is abundant in the type locality, where, in March, the number of specimens collected at bait exceeds all other species of *Lithophane* combined.

Etymology. The specific epithet *joannis* is the genitive case of the Latin word for John. John H. Newman, who introduced the second author to the study of Noctuidae, declined to be recognized with a patronym. Therefore, this species is named for the first word of the type locality—John Bryan State Park—which is also by intentional coincidence the first name of Mr. Newman.

ACKNOWLEDGMENTS

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The following individuals provided access to specimens in the collections under their care: Donald Azuma, Academy of Natural Sciences, Philadelphia, Pennsylvania; Julian P. Donahue, Los Angeles County Museum of Natural History, Los Angeles, California; John G. Franclemont, Cornell University, Ithaca, New York; George L. Godfrey, Illinois Natural History Survey, Champaign, Illinois; J. Donald Lafontaine, Canadian National

Collection, Ottawa, Ontario, Canada; Mark F. O'Brien, University of Michigan, Ann Arbor, Michigan; Robert W. Poole, National Museum of Natural History, Washington, D.C.; Eric L. Quinter, American Museum of Natural History, New York; John E. Rawlins, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; Roy W. Rings, Ohio State University, Ohio Agricultural Research and Development Center, Wooster, Ohio; Frederick W. Stehr, Michigan State University, East Lansing, Michigan; Yale Sedman; Barry S. Nichols; Mogens C. Nielsen; J. Richard Heitzman; Roger L. Heitzman; Jeffrey D. Hooper; Loran D. Gibson; William F. Babcock; George J. Balogh; and Donald J. Wright. We thank Douglas C. Ferguson and Robert W. Poole for reviewing the manuscript.

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GENERAL NOTES

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PARASITOID INDUCED MORTALITY IN THE EGGS OF THE ENDANGERED GIANT SWALLOWTAIL BUTTERFLY *PAPILIO HOMERUS* (PAPILIONIDAE)

Additional key words: Jamaica, Encyrtidae, Eulophidae, life history.

The giant swallowtail butterfly, *Papilio homerus* Fabricius, is confined to the Caribbean Island of Jamaica where it presently exists in two isolated and diminishing strongholds (Emmel & Garraway 1990). The numbers of *Papilio homerus* have been dwindling, and it now is listed in the IUCN Red Data Book as one of the four endangered swallowtail butterflies (Collins & Morris 1985).

Important contributions to our knowledge on the plight of *P. homerus* come from the works of Walker (1945), Emmel and Garraway (1990), and unpublished manuscripts by J. Parnell and T. Turner. None of these works, however, examine in detail, factors that might be controlling population numbers (Emmel and Garraway 1990). This paper presents the preliminary results of a survey investigating the importance of developmental mortality; here we examine the level of egg mortality due to parasitoids at a major population center.

This study was conducted at Fishbrook (near the village of Millbank) in the parish of Portland. The area is mainly secondary forest; large portions have been cleared over several decades for shifting cultivation. *Hernandia catalpaefolia* Britton and Harris, (Hernandiaceae) was the only larval food plant verified during this study. This plant is locally common in the damp ravines of the mountains of the parishes of Portland and St. Thomas and is endemic to this part of Jamaica. Adams (1972) recorded this plant between 450 m and 640 m elevation, but we recorded it as low 150 m.

One hundred and eight *Hernandia* trees were sampled. All leaves up to a height of 3 m above the ground were examined individually, and the following data were recorded: number of eggs observed, number of eggs hatched, and number of eggs attacked by various mortality factors. Sampling was done once a month from July to October 1991. The transfer of eggs from the field to the laboratory allowed for further examination and ensured that eggs were not counted more than once.

Females of *P. homerus* lay their eggs on the upper surfaces of the leaves. Most eggs or their remains persist for over one month, and it is quite easy to determine if a *P. homerus* egg has been attacked by parasitoids. Emergence holes of the parasitoids are small and round. Those of *P. homerus* larvae are larger and irregular in shape; occasionally the larva eat considerable portions of the chorion. Moreover, in parasitized eggs, larval exuviae and mummified larvae, pupae, or adults of the parasitoids were easily identified. Eggs without emergence holes were taken to the laboratory for study; examination under the microscope or hand lens revealed parasitoid ovipositional sites. All live material was allowed to develop.

Three species of hymenopterans, one member of the genus *Ooencyrtus* (Encyrtidae) and two of the genus *Chrysonotomyia* (Eulophidae), emerged from the eggs of *P. homerus*. *Ooencyrtus* sp. is undescribed and appears to be unlike any described species from the New World (Noyes pers. comm.). The genus *Ooencyrtus* is cosmopolitan; most species are polyphagous and are primarily parasitoids of the eggs of other insects, notably Heteroptera and Lepidoptera. The *Chrysonotomyia* spp. have not been identified to species; however, members of the genus *Chrysonotomyia* generally are parasitic on the eggs and larvae of phytophagous insects, mainly leaf-mining and gall forming Diptera and also Lepidoptera on herbaceous plants.

The parasitoids oviposited in the early stages of development of the *P. homerus* embryo while the contents of the egg were still fluid. Only once was the sclerotized remains of a

TABLE 1. Mortality of *P. homerus* eggs caused by parasitoids at Fishbrook, July to October 1992.

Month	No. of eggs	% eggs hatched	% eggs parasitized	% other mortality
July	258	9.3	79.5	11.2
August	108	17.6	71.3	11.1
September	63	19.0	76.2	4.8
October	14	7.1	64.3	28.6
Total	443			
Mean		12.6	76.5	10.8

P. homerus larva discernible in the remains of a parasitized egg. The larvae of the parasitoids generally consumed the contents of the egg and between 10 and 18 adult parasitoids generally emerged.

The parasitoids resulted in 76.5% ($n = 443$) egg mortality during the months July to October (Table 1). This is a significant portion of the 87.4% total egg mortality. The remaining 10.9% mortality was caused by fungus and a number of unidentified factors.

While the true role of the egg parasitoids is far from resolved, the 76.5% egg mortality they caused in this case is significant for an animal with extremely low densities. This suggests a very high efficiency in searching for *P. homerus* eggs or the possibility of alternate hosts that maintain the population of parasitoids at high levels. As pointed out by Parsons (1984), parasitoids breeding in a common alternate host may adversely affect the survival of a rare species.

We thank the Jamaica Agricultural Research Programme for financial support, and J. S. Noyes and J. LaSalle of the Commonwealth Institute of Entomology for identifying the parasitoids.

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WORLD DISTRIBUTION OF THE *VANESSA CARDUI*
GROUP (NYMPHALIDAE)

Additional key words: biogeography, migration, dispersal, *Vanessa kershawi*.

Vanessa cardui (Linnaeus) and *V. kershawi* (McCoy) together comprise the *cardui* group of the genus *Vanessa* (Field 1971). The two species are morphologically similar and are allopatric in distribution. *Vanessa cardui* is undoubtedly the most widespread butterfly in the world and is purportedly "cosmopolitan;" *Vanessa kershawi* is restricted to the Australian region. The purpose of this paper is to review and detail the distributions of these two species. The data for this review represent a variety of previously published sources too numerous to enumerate.

North, Central, and South America. *Vanessa cardui* is found throughout the United States from sea level along the California coast up to 3960 m on Pike's Peak in Colorado. It occurs sporadically across southern Canada from Newfoundland to British Columbia and rarely in northern Quebec (Fort Chimo), southeastern Northwest Territories (Baker Lake), and extreme southern Yukon (Carmacks). It is absent from Alaska, except in the extreme southeast (Chickamir River), and it does not occur above the Arctic Circle in the Western Hemisphere, except for one record from northern Greenland (Scott 1986). It is absent from all of the North American Arctic islands, including the Pribilofs and Aleutians. *Vanessa cardui* is found throughout Baja California and much of Mexico, especially the northern part (also Aguascalientes, Distrito Federal, Morelos, Vera Cruz, and Guerrero). In Central America it occurs in Guatemala (common in montane areas), Honduras, Costa Rica (rare in montane areas), and Panama (rare). It apparently is absent from most of South America; however, there are two records from high inter-Andean valleys in Ecuador (Scudder 1876, Brown & Heineman 1972).

Along the American west coast, *V. cardui* has been collected on the Queen Charlotte Islands, Vancouver Island, throughout the California Channel Islands, and several islands off the coast of Baja California, including San Martin, Cedros, and San Jose. It is apparently absent from Isla Guadalupe (Baja California), Islas Revillagigedos (Colima), and the Galapagos Islands (Ecuador).

In the Caribbean region, *Vanessa cardui* occurs on Bermuda (resident but rare), the Florida Keys (Siesta Key, Paradise Key, and Key West), the Bahamas (New Providence Island and San Salvador Island), Cuba (rare), Grand Cayman, Jamaica (rare), Hispanola (uncommon in montane areas), Puerto Rico (rare), and Mona (rare). In the lesser Antilles it occurs on Montserrat and rarely on Dominica, Martinique, St. Lucia, St. Vincent, Barbados, Grenada, Trinidad, Tobago, and San Andres Island.

Africa. *Vanessa cardui* frequently is cited as ranging throughout Africa and the Ethiopian region, but it is absent from Rio Muni and the Gulf of Guinea Islands. It has been reported from Morocco, Algeria, Tunisia, Libya, Egypt, Ethiopia (up to 3350 m), Sudan (up to 3050 m), Dakar, Senegal, Liberia, Sierra Leone, Ghana, Nigeria, Congo, Kenya, Uganda, Rhodesia, Nyasaland, Malawi, Mozambique, Bechuanaland, South-West Africa, and South Africa (to the Cape of Good Hope at Cape Town, Port Elizabeth, and East London). Records from the Sahara region include northwest Sahara, Ahaggar, Air, and Tibesti.

Mediterranean, African, and Indian islands. *Vanessa cardui* is found throughout the Mediterranean and many of the Aegean islands, the Azores, Madeira, Canary Islands, Cape Verde Islands, Ascension, St. Helena, Tristan da Cunha (one record), Madagascar (common), Reunion, Mauritius (rare), Seychelles (Mahe, St. Anne, Aldabra, Assumption, Coetivy, Desroches), Socotra (common), Bahrain, Maldives (North Male Atoll, Hulule Island, Addu Atoll), Sri Lanka, Andamans (South Andaman), Nicobars (Nancowry), and Christmas Island. In the South Atlantic it is absent from Fernando Noronha, and it is unreported from the Comoro Islands.

Europe. *Vanessa cardui* ranges throughout Europe. Although it is more common in the southern portion of the continent, it is known from Scandinavia and Finland to above the Arctic Circle in Lapland. In the North Atlantic it occurs throughout Great Britain, on the Scilly Islands, Channel Islands, Isle of Wight, Isle of Man, Ireland (rare), Outer Hebrides, Orkneys, Shetlands, Faeroes, Iceland (rare), and Spitsbergen.

Middle East and Asia. In the Middle East, *Vanessa cardui* is known from throughout the Arabian Peninsula, Kuwait, Iraq, Jordan, Israel, Lebanon, Syria, Turkey, Transcaucasia, and Iran (up to 3350 m). On the Asian continent it occurs in Afghanistan, Pakistan (up to 5180 m), India (throughout), Nepal (3960 m on Mount Everest), Sikkim, Bhutan, Himalayas, Burma, Thailand (rare), Laos (rare), North Vietnam, Malay Peninsula (sporadic), northeastern Sumatra (common in montane areas), Nias, Java, Singapore Island, Palawan, the Philippines, Taiwan, and Hainan. *Vanessa cardui* is absent east of Wallace's Line. It occurs throughout Russia (including Siberia and Far East USSR, sporadic in places) except for the Far North, and ranges above the Arctic Circle in western Siberia. It also is found in Tibet (up to 5030 m), Yunnan (2900 m), central, west, and north China (including Manchuria and Amur), Hong Kong, Mongolia, Korea, Quelpart Island, Cheju-do, many small islands along the west coast of South Korea, Ryukyu Islands, Japan, Sakhalin, and the Kurils.

Pacific Islands. With the exception of its introduced and naturalized status on Hawaii (Kauai, Oahu, Molokai, Maui, Lanai, and Hawaii), it is conspicuously absent from Pacific Islands, including Micronesia, Melanesia, and Polynesia. The male and female genitalic structures of specimens from Hawaii are identical to those of *V. cardui* and differ from *V. kershawi* (Zimmerman 1958, Field 1971), thus casting doubt on the theory that Hawaiian stock is intermediate between the two (Walker 1919, Scott 1986).

Australia. *Vanessa cardui* is unknown from Australia except in the extreme southwest corner at Bunbury and Rottnest Island (Barrett & Burns 1951) near the major seaport of Perth—most likely the result of an introduction.

Migrations at sea. Migrating *V. cardui* sometimes are observed from aboard ships crossing the ocean; flights have been reported from various locations in the Mediterranean Sea. A huge migration appeared suddenly along the Riviera in May 1918 (Morris 1919), and NW migration was noted flying out over the Mediterranean from Gaza in April 1917 (Pendlebury 1921). Small groups sometimes fly in from the north in September along the Egyptian coast, and there was a sudden appearance of a migration on Malta in 1952 (Valletta 1952). Singletons have been observed in the Indian Ocean 400 km SE of Arabia; 400 km NNW of Cape Amber, Madagascar; 190 km W of Bombay; and 515 km W of the Laccadives. About 100–190 km off the African coast, migrating individuals were sighted at numerous locations between Morocco and Portuguese Guinea in September 1943 (Williams 1945). Other sightings include numerous individuals 965 km from Gambia and 320 km from the Cape Verde Islands. One individual was observed alive and floating on the water and another flying around a ship 800 km E of Newfoundland in August 1865, and six were seen 2250 km W of the Saharan coast (23°N, 41°W) in October 1950 (Williams 1965).

Broodedness and overwintering. *Vanessa cardui* is continuously brooded and does not diapause. During the winter months its huge range contracts to below about 35°N latitude in the North Hemisphere, at least in Europe and North America; it recolonized northward by migration again each spring. It overwinters along the extreme north African coast in Morocco and northern Algeria, and more extensively along the western margin of the Red Sea and in Saudi Arabia (Baker 1978). In North America it overwinters in the Sonoran and Chihuahuan deserts (C. J. Durden & K. Roever pers. comm., Bender 1982). It also overwinters in southern Africa, at least in Malawi and Rhodesia, migrating southward in the spring.

Vanessa kershawi. *Vanessa kershawi* is common throughout southern Australia below the Tropic of Capricorn, occurring less commonly to 20°S in the west, 23°S in the center, and 16°S in the east of Australia. It is uncommon in Queensland and absent in the far north and in the Torresian faunal province, except in the SE part (Common & Waterhouse 1972). The butterfly is found in Tasmania (up to 915 m), including Hobart. Two worn "waifs" were collected in May 1906 on Cocos-Keeling Atoll in the Indian Ocean (Jones

1909). On the Great Barrier Reef, Queensland, it is known from Lindeman Island north of 21°S, and from Percy, North West, and Wiggins Islands south of 21°S (Duckworth & McLean 1986). In New Zealand, it probably is not resident, but it becomes common and widespread there occasionally following periodic migrations from Australia. It is recorded from North Island, South Island, and Stewart Island. It also has been reported from Lord Howe Island (sometimes common), Norfolk Island (in 1968), New Caledonia and New Hebrides (Walker 1919), Lifu in the Loyalty Islands (Walker 1902), and Suva on Viti Levu, Fiji (Robinson 1975). There are few observations of *V. kershawi* at sea, although multitudes were seen off Cape Otway in the Bass Strait in November 1860, and one was sighted at 35°10'S, 155°40'E off New South Wales in November 1904 (Williams 1930). In late September to early October 1889, they covered "the gear and decks of ships many miles out to sea" from a large migration flying SE from Victoria (Rainbow 1907).

Summary and conclusions. The incredibly vast range of *V. cardui* lies primarily within the Northern Hemisphere, extending substantially into the Southern Hemisphere only on the African continent; it occurs from sea level to about 5200 m in elevation. *Vanessa kershawi* is confined to the Australian continent where it completely replaces *V. cardui*. Their closest geographical approach is on Cocos-Keeling Atoll (*V. kershawi*) and Christmas Island (*V. cardui*) as waifs. The frequent claim that *V. cardui* is a cosmopolitan, worldwide butterfly is unwarranted, although it certainly is the most widely ranging species known.

Neither *V. cardui* nor *V. kershawi* is polytypic, i.e. there are not recognized subspecies. This probably reflects the fact that both are strongly migratory, a behavior that acts to inhibit localized population differentiation.

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NOTES ON THE TYPE OF *PAPILIO CRESPHONTES* AB. "MAXWELLI" (PAPILIONIDAE)

Additional key words: aberration, holotype, Florida.

Papilio cresphontes (Cramer) is a widespread Neotropical species with few associated infrasubspecific names, despite the preponderance of these names employed elsewhere within the Papilionidae. *Papilio cresphontes* ab. "maxwelli" Franck is a rare aberration characterized by elongated yellow spots near the apex of the forewing, described by Franck (1919a) as "giving the specimen a striking tropical appearance." In his description of the taxon, Franck (1919a) figured the holotype of "maxwelli" but omitted data regarding the type locality, sex of the specimen, and the collection in which it was deposited. As a result, this information was unknown to subsequent authors, including Miller and Brown (1981) and Ferris (1989). Kimball (1965), likewise, did not mention *P. cresphontes* ab. "maxwelli", apparently because he was unaware of the Florida type locality. However, Franck (1919b) amended his description with a short note that has been overlooked by researchers for over seventy years.

In a one-sentence emendation, Franck (1919b) designated the type locality as St. Petersburg, Florida, and noted that the description was based upon a single male specimen in the William Barnes collection. The holotype is now located in the collection of the National Museum of Natural History where the Barnes collection is largely deposited. The specimen possesses two labels: a red holotype label affixed in 1990 and an old white label bearing nearly undecipherable handwriting, possibly reading "Mar 29." No additional information is discernable. Clark (1936) figured another male specimen of the "maxwelli" phenotype without providing locality data.

Although infrasubspecific taxa are not subject to rules of the International Code of Zoological Nomenclature, any taxon within such a highly popularized and thoroughly studied family is of special interest.

I thank Robert K. Robbins for his assistance in locating the type specimen.

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BOOK REVIEWS

THE NEPTICULIDAE AND OPOSTEGIDAE (LEPIDOPTERA) OF NORTH WEST EUROPE. Fauna Entomologica Scandinavica, Volume 23, part 1 (text), part 2 (plates), by Roland Johansson, Ebbe S. Nielsen, Erik J. van Nieukerken, and Bert Gustafsson. 1990. E.J. Brill/Scandinavian Science Press Ltd., Leiden, New York, Kobenhavn, Köln. 739 pp., 111 + 1122 figures. Hardcover, 14.5 × 21 cm, ISSN 0106-8377; 55 Dutch Guilders (about \$30.00 U.S.)

As quality standards for systematic publications improve and new technologies become available, it becomes increasingly difficult for a single author of a monographic treatise to meet those standards or fully utilize those technologies. These challenges are often complicated further by a general downward trend in financial support for monographic studies. One obvious solution to such a dilemma is multiple authorship. A proper combination of co-authors—each providing their special expertise—can vastly improve as well as expedite a major work. This recently published two-volume review of the Nepticulidae and Opostegidae of North West Europe is a good example of what balanced cooperation among several authors can produce.

Although technically an "amateur," the senior author of this work, Roland Johansson, contributed significantly not only as a result of his lifelong interest in the systematics and natural history of Nepticulidae, but also by drawing the 186 beautifully executed color illustrations of the adults and over 900 line drawings. Ebbe Nielsen's general knowledge of most monotrysian families was an asset particularly in the preparation of the introduction and in co-authoring the section on the tribe Nepticulini. Nielsen also became the major editor and coordinator for the project. Erik van Nieukerken, certainly one of the leading researchers on Nepticulidae today, is acknowledged as being responsible for much of the most recent information on the evolution and higher classification of the Nepticulidae. The depth of his contribution is obvious to anyone familiar with his outstanding paper on the "Systematics and Phylogeny of Holarctic Genera of Nepticulidae" (Zool. Verh. Leiden 236:1-93; 1986). Nieukerken was also the author of the section Opostegidae. Bert Gustafsson's knowledge of larval Nepticulidae is reflected in the emphasis on larval morphology and systematics evident in this work.

The Nepticulidae and Opostegidae are among the smallest Lepidoptera in the world. The wing span of the smallest measure less than 3 mm. Because of their size they are not an easy group to work with and are especially difficult to dissect and to rear. Despite these obvious obstacles, as many amateurs as professional entomologists have concentrated on these tiny moths in Scandinavia, with the result that the Scandinavian nepticulid fauna is the best researched in the world. This work treats 121 species of Nepticulidae (ca. 20% of the known world fauna of nearly 600 species) and 4 species of Opostegidae (ca. 4% of the known world fauna of 102 species) in an area including Fennoscandia south to Paris, France, and the British Isles to and including Poland and the Baltic republics. Only 120 species of Nepticulidae are enumerated in the checklist (pp. 60-62) and elsewhere in the text because, for reasons unclear (a late insertion?), *Stigmella betulicola* (Stn.) and *S. nivenburgensis* (Preiss.) are listed as 6a and 6b respectively.

Most of the first 76 pages of the text are devoted to introductory material, which provides one of the best available summaries of the different life stages of the Nepticulidae. Reviewed in this section are the morphology of the adult and immature stages, biology, phylogeny, and distribution. Under biology, special emphasis has been devoted to host-plant relationships, parasitoids, and predators, with shorter discussions on ecology and conservation. The phylogeny of the Nepticuloidea is briefly reviewed at the family and generic levels (pp. 57-59) and is largely based upon the more extensive, manually derived treatment by van Nieukerken (1986), referred to above. Species keys are provided not only to the adults according to customary taxonomic groupings and based upon superficial male and female characters and male genitalia, but also according to host genera and larval/mine morphology. In addition, a brief synopsis for each species group is provided for the largest tribe, Nepticulini.

The species treatments are informative and concise with a strong emphasis on life

history. The latter represent an accumulation of knowledge for Nepticulidae unequalled for any other comparable region. The larvae are treated by Gustafsson and van Nieukerken in a separate section from the adults. Descriptive synopses, supplemented by numerous, selective line drawings are provided for 101 of the total fauna of 121 species. The immature stages of only six, mostly rare species are completely unknown. Table 3 on pages 325–327 provides an excellent summarization of the body chaetotaxy for the 101 species studied. The main text of volume one concludes with the section on Opostegidae authored by van Nieukerken. Only two genera and four species of Opostegidae are represented in the region covered by this series. Finally, the general distribution of each nepticulid and opostegid species is graphically summarized in a chart on pages 388–401. The text appears to be well edited, with a few typographical errors noted (e.g., on page 37, the dorsal calli referred to in text figure “58” should read “60”).

Because of the superb, collective expertise of all four authors and the relatively copious knowledge of the Nepticuloidea for the region treated, the importance of this publication exceeds that of a major faunal contribution. This work should be regarded as a primary source for anyone seeking information on the general biology and morphology of Nepticuloidea.

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DISTRIBUTION OF BUTTERFLIES IN NEW MEXICO (LEPIDOPTERA: HESPERIOIDEA AND PAPILIONOIDEA), by Michael E. Toliver (edited by Richard Holland), 1977 (1991). Published by the authors. Distributed by R. Holland, 1625 Roma NE, Albuquerque, New Mexico 87106. 239 pp., 1 text figure. Soft cover, spiral bound, 22.45 × 28 cm., no ISBN; \$10.00 (postpaid).

As one who has attempted to compile butterfly records for a large geographic entity, I recognize the *Distribution of Butterflies in New Mexico* as a labor of love. It is rare that information accumulated in one's notebook evolves into an invaluable printed list available to anyone interested in the region. Such compilations form a solid foundation for future investigations, be they distributional, ecological, or biogeographical. In addition, they provide a basis for planning trips by the general collector.

A short introduction is followed by species accounts presented in order of the checklist of C. F. dos Passos (1964, *Lepid. Soc. Mem.*, No. 1, 145 pp.), with specific location (listed by county), date, and source of the record. A literature cited section and an index by specific name, keyed to dos Passos (1964 *op. cit.*) checklist number, completes this volume. The major shortcomings of the list (14 years between completion and published appearance, nomenclature similarly dated), are noted by Holland in the preface. Collectors should be aware that the book does not incorporate the recent renumbering of most state highways.

The data were assembled by Mike Tolliver and include those for 269 species of butterflies through 1977; by early 1992, the butterflies known from New Mexico had increased to 314 species (*vide* R. E. Stanford). The majority of the records are those of the author and editor; these are taken at face value. Literature and other records are presented with or without comment; it would be helpful to know which, if any, were further verified, especially single state records or those from apparently extralimital localities. For example, why were the putative specimens of *Papilio troilus* not examined? The problem with the supposed New Mexico records of *Speyeria hydaspe* is mentioned; a similar problem for *Speyeria zerene* is not (see Scott, J. A., 1986, *The butterflies of North America*, Stanford Univ. Press, 583 pp.). One wonders why the determinations of *Systasea zampa* were not

verified and it is unfortunate that specimens of the *Erynnis persius* complex were not dissected.

The nomenclature, as stated in the introduction, is largely that of dos Passos (1964 *op. cit.*) and was updated, apparently by Holland, to include many (but not all) subsequent revisions. New subspecific names proposed for *Euphydryas anicia* by C. D. Ferris and R. Holland (1980, Bull. Allyn Mus., No. 57), *Speyeria atlantis* by R. Holland (1988, Bull. Allyn Mus., No. 115), and *Colias alexandra* by C. D. Ferris (1988, Bull. Allyn Mus., No. 116) are included, yet the revisions of *Neominois ridingsii* by G. T. Austin (1986, Bull. Allyn Mus., No. 107) and *Thessalia fulvia* by M. J. Smith and J. P. Brock (1988, Bull. Allyn Mus., No. 118) were not consulted. In certain instances, subspecies of some taxa are not recognized. *Eurema mexicana* is treated as monotypic, yet the southern Central American *E. m. bogotana* is certainly distinct. The *Phoebis sennae* is probably *P. s. marcellina*. No subspecies are mentioned for *Calephelis nemesis* or *Vanessa atalanta*. New Mexican *Pontia beckerii* must be of the nominotypical subspecies; *P. s. pseudochloridice* is a Pacific Northwest taxon. *Cyllopsis henshawii* is a subspecies of *C. pyracmon* and the name "nabokovi" refers to the fall brood phenotype (see Scott 1986 *op. cit.*).

Typographical errors are relatively few although I did not specifically search the book for these. At least one literature citation, C. F. dos Passos and L. P. Grey (1947, Amer. Mus. Novit., No. 1370), was omitted.

All these criticisms are minor. As Holland states in the Preface, "for sheer volume of information it will almost surely never be surpassed." The deficiencies of this work do not in any way detract from its importance and usefulness in the continuing study of the butterflies of New Mexico and southwestern United States.

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SIMON & SCHUSTER'S GUIDE TO BUTTERFLIES AND MOTHS, by Mauro Daccordi, Paolo Triberti, and Adriano Zanetti (originally published in Italian under the title *Farfarelle*, translated into English by Arnoldo Mondadori). 1988. Simon and Schuster/Fireside Books. Printed in Italy, published by Simon & Schuster, Inc., Rockefeller Center, 1230 Avenue of the Americas, New York, New York 10020 USA. ii + 383 pp., 29 text figures, 1 table, 289 color plates. Soft cover, 11.5 × 19 cm, ISBN-0-671-66066-7; \$11.95 U.S.

What a refreshing little book. Oh come on, you say, a field guide to the butterflies and moths of the world? You can't be serious. Obviously, with a genre limit of several hundred pages, a comprehensive field guide on any particular subset of the world Lepidoptera is out of the question. The point of such a field guide should be to stimulate and enrich the large mass of humanity that has minimal lepidopterological experience. This is no small task, but one at which Daccordi et al.'s volume excels.

Consider the first paragraph of the Introduction. That's as far as one might realistically expect many uninitiated readers to advance before abandoning text forever in favor of color plates. If a book hasn't awakened the audience's interest after those first few sentences, it's finished. The authors know this well. In just one paragraph they move from the aesthetics of butterflies and moths, to their more striking biological attributes, to their ties with the plant kingdom, to agriculture and human culture—while all the time developing a low-keyed yet alluring appeal for conservation and ecological awareness. It is a deft example of how to mix the author's agenda with that of the reader.

In fact, this is one of the clearest, most refreshingly honest and articulately crafted general natural science books I've reviewed. To see what I mean, focus on the first sentences that follow each section heading in the first 69 pages of introductory/background material. Evolution: "We have gained little knowledge concerning the evolution of the Lepidoptera.

This is hardly surprising if we consider the delicacy and fragility of the body of these insects, the only (and very rare) parts left as recognizable fossil remains [p. 11].” Habits: “If we examine the flight of a butterfly or moth and the crawling movements of a caterpillar, we might be tempted to think that most of the activities of these insects are ruled by chance [p. 31].” Predators and parasites: “In the life cycle of a butterfly or moth, no stage of development is immune to the attacks of parasites and predators. Among the former, above all, are viruses and bacteria, as yet little known, which are the principal causes of death in caterpillars [p. 51].” The reader gets sucked into these stories, as if this were a paperback whodunit.

I’m biased, of course, but can gleefully report here an overarching focus on moths rather than butterflies throughout the 323 color figures. For example, among the larval shots are 10 butterflies and 24 moths, and 7 of the latter are casebearers, leafrollers, and other perhaps less glamorous microlepidopterans. Perhaps . . . but you can’t appreciate the role of a casebearer in the grand scheme of things if you don’t know what one is. The offbeat lepidopterans are prominently displayed, too. There is a wonderful picture of an apterous adult female geometrid (Plate 101), the fuzzy and cuddly teddy bear of the book; a contorted adult lappet moth (Plate 70) to convince even the most skeptical that crypsis happens; and an incurvariid (Plate 37) with antennae quintuple the body length to underscore that wings aren’t necessarily always where it’s at. All in all there are 323 species accounts, of which 34 illustrate the larval stage and 289 the adult stage. Most photographs are of live organisms and the color reproduction is excellent.

The species accounts are organized by major geographic region of the world, and therein in alphabetical order by genus. The blurbs accompanying the photos are reasonably well organized, quite informative, and adorned with colored icons indicating the type of lepidopteran (diurnal, nocturnal, micro), the general habitat, and localization within the geographic region in question. There are a few mistakes in identification (the *Catocala* that isn’t on Plate 153; the spicebush swallowtail that ate pipevine on Plate 189), but by and large I don’t think such mistakes mean anything in this sort of volume. The identification error rates are higher for regions other than the Palearctic, from whence the authors hail, which isn’t surprising.

For such an otherwise well produced book, there are still a few perplexing inconsistencies. Thus, for some reason *Grammia virgo* (Plate 144) warrants an additional subtitle—“(formerly *Apantesis virgo* L.)”—the taxonomic significance of which is never explained. And Raja Brooke’s Birdwing (*Trogonoptera brookiana*, Plate 288) and the Dogface (*Zerene caesonia*, Plate 208) don’t seem to warrant subtending common names. But the largest problem by far is the sprinkling of photos of dead adult Lepidoptera alongside those of the living: for example, a scintillating translucent *Cithaeris* savoring a plant stem in the dark forest, next to a rigid *Danaus* flopped onto some twigs (Plates 219–220); or a streamlined *Xylophanes* sphingid, forced to cohabit with the aforementioned and quite dormant Dogface (Plates 207–208). The effect is just awful, and the liability to the book’s educational appeal is anything but trivial. It is an entirely unnecessary and avoidable scar on an otherwise fine volume.

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Journal of the Lepidopterists’ Society
46(3), 1992, 243–244

LARVAE OF OWLET MOTHS (NOCTUIDAE): BIOLOGY, MORPHOLOGY, AND CLASSIFICATION, by O. I. Merzhheevskaya (original release 1967) (translated from Russian by P. M. Rao; Scientific Editor, George L. Godfrey). 1989. Distributed by E. J. Brill Publishing Company, P.O. Box 9000, NL-2300 PA Leiden, The Netherlands; U.S.A. & Canada, E. J. Brill (U.S.A.) Inc., 24 Hudson Street, Kinderhook, New York 12106. xx + 419 pp., 97 text figs., 6 tables. Hard cover, 15 × 24 cm, ISBN 90 04 08804 0; \$57.50 U.S.

You have to admire anyone who decides to dive headlong into the bottomless pit that is the systematics of the Noctuidae. But, to purposely delve into the documentation and identification of the immature forms borders on insanity. I am assured by George Godfrey in his Forward to the English-language Edition that the author, Olga Ivanovna Merzhchevskaya, was a well respected teacher and researcher and definitely in full charge of her considerable faculties. In fact, this study on the biology and morphology of larvae of 144 species of Noctuidae from Belorussia is a testament to her patience, perseverance, and detailed observations.

The author was able to compile information on each larval instar of a given species so that she could describe the changes in morphology and patterning during growth and development. This adds much to the knowledge of immature noctuids.

Also of note are the brief descriptions of the eggs, plus data on where and how they were deposited. How useful it would have been if scanning electron micrographs were provided for visual comparisons. Based on the attention to detail that characterizes her work, S.E.M. technology must not have been available to her.

Godfrey indicated—and I concur—that a weakness is inherent in the identification keys because of their reliance on color patterns. Although the author used a fixative made of ethyl alcohol, salicylic acid, common salt, and water to maintain color in preserved specimens longer (up to six months for the more labile pigments; over five years for melanic patterns), the keys require last instar larvae that have been recently preserved. Still, I have yet to try this fixative but definitely intend to do so.

This book was originally published six years prior to Godfrey's thorough study of the larvae of the noctuid subfamily Hadeninae (1972). Had Godfrey's study been available to Merzhchevskaya, she may not have decided to disregard the characters of the hypopharyngeal complex, which she considered not useful for taxonomic purposes.

Overall, the study has far more positives than negatives. Additionally, the English translation of the work is excellent. There is nothing left to be deciphered or reinterpreted that I could find. This publication is certainly a worthwhile contribution to the slowly growing body of knowledge on juvenile stages of Lepidoptera. It should be on the shelf of all serious students of the biosystematics of Lepidoptera and of those interested in the taxonomy of larval insects. The host plant information, life histories, and biological data are useful to an even broader audience.

Only a few who have ventured into this realm are still so engaged. These bold scientists are to be both admired and pitied. But don't let me dissuade any aspiring student. On the contrary, jump in and get wet; there's a lot of water; it's sort of calm, and it's plenty deep.

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DISCOVER BUTTERFLIES! AN ACTIVITY BOOK FOR FAMILIES, STUDENTS, AND TEACHERS, edited by LuAnn Craighton, Project Coordinator. 1991. Callaway Gardens, Ida Cason Callaway Foundation, Pine Mountain, Georgia 31822. iv + 61 pp., color covers, black & white illustrations, tables, and diagrams. Softcover, 22.0 × 28.0 cm, no ISBN; \$7.95.

Since its opening in 1988, the living butterfly displays and museum exhibits at the Day Butterfly Center in the Callaway Gardens of western Georgia have educated hundreds of thousands of visitors about the wonderful fascination of butterflies. Now the Education Department of the Ida Cason Callaway Foundation, under the direction of Lepidopterists' Society member LuAnn Craighton as Project Coordinator, has produced this exciting activity book on the world of butterflies. The book is accompanied by a "Butterflies" videotape (available separately at \$19.99, or as a package of activity book and video for

\$24.95). The combination package will be of interest to every lepidopterist who wants to interest other members of his or her family, friends, students, and associates about butterflies. The book and video set should also become a very popular and useful resource in schools, summer camps, and similar educational programs.

The book includes six chapters focusing on the biologically important aspects of butterflies, especially their life history, ecology, conservation, and behavior. Chapter 1, "Butterfly Basics," covers butterfly classification, very basic anatomy, the structure and purpose of colors on wings, and suggested activities on these subjects (such as butterfly family flash cards, building your own butterfly, and determining whether you have a butterfly or a moth at hand).

Chapter 2, "Metamorphosis," describes the life history of butterflies. Activities include building an insect cage, rearing your own butterflies, and acting out the life cycle of a butterfly.

Chapter 3, "Butterfly Behavior," includes discussion of courtship and mating, basking, flight, roosting, feeding, and puddling. Activity instructions range from writing poetry about butterfly behavior to timing the flight speed of adult butterflies.

Chapter 4, "Butterfly Conservation," conveys effectively a number of concepts on the ecological importance of butterflies, facts on the distribution and biodiversity of butterflies, and even a pitch for saving the world's rainforests. Activities in this chapter include working on understanding food webs and other important concepts in ecology.

Chapter 5, "Marvelous Monarchs," is a more concentrated look at a single species, the monarch butterfly. Activities here even include tagging monarchs to study the migratory habits of monarchs through a capture, tag, and release program. It also includes an activity to help make the monarch our national insect by writing letters to senators and representatives.

Chapter 6, "Butterfly Watching," includes not only suggestions on how to watch and collect butterflies but also a discussion of careers as entomologists, the drives to name state butterflies, and some of the uses of references in studying butterflies. One of the fine activities described in this chapter is how to plant your own butterfly garden, including choices of plants, locations, and design, and how to use biological controls and insecticidal soaps for pest management.

The book ends with a comprehensive list of popular resources and references, including most of the current butterfly and moth field guides, butterfly gardening resources, biological supply companies, children's books, and organizations (including the Lepidopterists' Society and its address). Living butterfly exhibits listed include the Day Butterfly Center, Butterfly World (Coconut Creek, Florida), and Marine World Africa U.S.A. (Vallejo, California). Bound in the center of the book is a folded removable poster that depicts butterfly anatomy on one side and the life cycle of the Zebra Longwing (*Heliconius charitonius*) in color on the other.

Although the field of lepidopterology has long enjoyed a plethora of technical books and other publications on butterflies and moths, and some coloring books that introduce young children to the diversity and distribution of butterflies in the United States and Europe, *Discover Butterflies!* makes an important contribution toward providing an integrated package for young novices, families, students, and teachers to learn more about butterflies. In combination with the colorful and stimulating 15-minute video, this book will indeed achieve the Callaway Foundation's purpose: to give people an increased respect for our natural world, and a heightened awareness of man's responsibilities to the world around us. It is exciting indeed to see butterflies used so effectively in this video/workbook learning package, and I predict it will be widely adopted. I recommend it as a gift to families with young children, and also as an appropriate gift to teachers at local elementary and middle schools, or to naturalist staffs at summer camps and nature centers, to encourage the incorporation of butterfly study materials in children's curricula.

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BIOLOGÍA Y MORFOLOGÍA DE LAS ORUGAS: LEPIDOPTERA, Vol. 6: Syssphingidae—Saturniidae—Endromidae—Lasiocampidae—Drepanidae—Thyatiridae—Notodontidae—Hypsiidae, by Carlos Gómez de Aizpúrua. 1988. Boletín de Sanidad Vegetal, Fuera de Serie No. 12. Published by Ministerio de Agricultura, Pesca y Alimentación, Centro de Publicaciones, 1 Paseo de la Infanta Isabel, 28014-Madrid, Spain. In Spanish. 248 pages, 402 color photographs. Soft cover, 18.5 × 25 cm, ISBN 84-7479-722-5; 3000 pesetas (about \$30 U.S.).

This book is part of a series on insect larvae published in Spain by the Ministry of Agriculture, Fisheries, and Nutrition as a volume in their Bulletin of Plant Protection. Its primary intended use is undoubtedly in the applied areas of entomology like agriculture and forestry, but the value of this book to taxonomists and lepidopterists also will be good. I have not seen the other volumes.

For each of the 50 species of Spanish moths treated, there is a map of the distribution in all of Europe, a graph of the 12 months showing the seasonal life cycle, a table listing morphological characteristics (more on color and pattern than on structure) of their caterpillars, a brief bibliography, and 8 or more color photographs, interspersed throughout the text. The greatest appeal and value of this book are these abundant and excellent photographs of caterpillars. For virtually all species the pupa, adult (usually one pinned and spread, one in living repose), and top and side views of the mature larva are shown. Lepidopterists interested in lasiocampids and notodontids will delight in seeing the 21 species of Lasiocampidae and 13 species of Notodontidae that fly in Spain displayed in so many fine color photographs. Interestingly, few cocoons are shown, the pupae having been extracted from their cocoons to be photographed. Good life history data are given in the text, including foodplants, flight times, and habitats, classification, and historical facts. There are no overall introductory chapters, but short ones for each family, and an index at the end.

The genus *Malacosoma* is usually misspelled as *Malocosoma* in this book. The type-species *M. franconica* is erroneously attributed to Esper, instead of to Denis & Schiffermüller, an error perpetuated by many authors (see Fletcher, D. S. & I. W. B. Nye, 1982, *In* Nye, I. W. B., ed., *The Generic Names of Moths of the World*, Vol. 4. Brit. Mus. Nat. Hist., London, xiv + 192 pp.). In the saturniids, I noted errors on the range maps for two: *Saturnia pyri* does not occur in the British Isles and the introduced *Samia cynthia* is not widespread across the northern edge of Africa. Therefore, I suspect that there are errors on maps for other species less familiar to me.

It may be of interest here to explain the historical reason why some European authors persist in classifying *Actias isabellae*, and sometimes *Aglia tau*, under the family name Syssphingidae, instead of Saturniidae. In the standard reference series edited by A. Seitz, *The Macrolepidoptera of the World*, Max Draudt in his 1930 volume apparently could not force himself to classify *Copiopteryx* and *Actias* into separate subfamilies, the long-tailed hindwings that they share convincing him (erroneously) of a relationship. So he put them together in Syssphingidae (which we now call Arsenurinae plus Ceratocampinae, within the Saturniidae) where *Copiopteryx* belongs but *Actias* does not. Standard references are all too often considered to be "the last word" in taxonomy, so here confusion persists 62 years later! Another taxonomic point I take this opportunity to make is that on phylogenetic grounds alone, the generic name *Graellsia* must be considered a synonym of *Actias* (because to separate out the European species leaves the American and Asian ones as a paraphyletic, i.e. unnatural, assemblage), although technically the two names are subjective synonyms (see Nässig, W. A. 1991, *Nota Lepid.* 14:131-143.).

This volume and probably the others in the series would be fine to add to the shelves of all European entomological libraries and also worthwhile to many non-European

lepidopterists. The quality and usefulness of the many color photographs should overshadow any difficulty or inability by some to read Spanish.

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OBITUARY

JOSÉ VALENTÍN HERRERA GONZÁLEZ (1913-1992)

Don José Herrera G., or Pepe, was born in Mejillones, Antofagasta Province, Chile, on 9 October 1913. His father, Juan Herrera Marín, and his mother, Isabel Gonzalez Del Rey, were born in Spain. He had three brothers, still living in Chile, and a sister who died in 1941.

Pepe married Doña Ernesta Dick Gandolfo from Puerto Natales in 1941. Ernesta had a pet mountain lion, beautiful portraits of which hang in several rooms of the Herrera home in Santiago, and the Herrera household always included one or more cats. Their first daughter, Nievas, was born in August 1942, daughter Carol in August of 1946, and daughter Verónica in December 1947. Nievas now lives in California. Carol and Verónica remain in Santiago. Pepe had 6 grandchildren, 2 girls and 4 boys, when he died after a short illness at his home in Santiago on 29 January 1992, at the age of 78. The world has lost a fine Lepidopterist; Chile has lost a fine educator; and many of us have lost a fine friend.

PROFESSIONAL CAREER

Pepe attended high school at the Colegio San Luis in Antofagasta city, and in 1931 entered the Instituto Pedagógico de la Universidad de Chile in Santiago, graduating with honors in 1934 as Profesor de Estado en Biología y Química. He then enrolled in the Instituto de Educación Física at the University and received a Professor of Physical Education degree in 1936. He was offered a post in Punta Arenas where they needed a teacher in science and physical education at the boy's high school, Luis Alberto Barrera. He accepted for six months, but stayed for ten years.

When he returned in 1946 to Santiago from Punta Arenas, Don José joined the faculty of the University of Chile as Professor of Zoology in the Institute of Pedagogy in 1946, and Profesor de Entomología in 1956. He then joined the Facultad de Filosofía Y Educación as chief of the Departamento de Biología from 1956 to 1960, and as Director del Centro de Estudios Entomológicos in 1960. He was elected Profesor Extraordinario de Entomología by the faculty of Philosophy and Education of the University of Chile in 1964.

In 1981 he joined La Academia Superiór de Ciencias Pedagógicas de Santiago as Professor in the Basic Sciences Department, becoming Emeritus Professor in 1982. He was a member of the board of directors of the Academy from 1981 to 1984. Pepe accepted the post of Director of the Entomological Center in 1984, then Director of the Entomological Institute (which he founded) in 1985.

In 1985 Don José was awarded the National Prize for Education, Chile's highest recognition in education. This award carries with it, aside from the considerable academic honors, a substantial life-time stipend for him and later, for his surviving widow. This award made from page news from Antofagasta to Punta Arenas and the magazine *Revista de Educación* featured him on the cover and in two articles of the October 1985 issue, as the nation remembered the fifty years of teaching by Profesor José Herrera G.

Pepe retired several times but was talked into taking up another academic post. Thus, he was asked to serve as Dean of Basic Sciences at the Universidad Metropolitana de Ciencias de la Educación, which he accepted in April of 1986 and held until his death.

The former journal *Publicaciones del Centro de Estudios Entomológicos*, which ran for 12 volumes until 1982, was succeeded and continued in 1986 as the new *Acta Entomológica Chilena*, Volume 13. As the Director of the Center for Entomological Studies and then as Director of the Entomological Institute, Don José was a major force in the creation of this new journal and he wrote its preface.

Pepe joined La Sociedad Chilena de Entomología in 1934 and was elected Vice-President in 1981. He had been a member of The Lepidopterists' Society since 1949 and served on the Executive Council from 1953 to 1955, and as Vice-President in 1966-1967. He joined the Sociedad de Biología de Chile in 1978, the Lepidoptera Research Foundation



Prof. José Herrera G.

in 1984, and was a member of the Advisory Council of the Association for Tropical Lepidoptera since its inception in 1989.

LEPIDOPTEROLOGICAL INTERESTS

Pepe was an educator, and his bibliography reflects this somewhat. In this capacity he travelled widely, allowing him to collect insects and visit many museums and entomological colleagues in Europe and North and South America. In 1951, from June through September, Pepe visited the United States and worked at the U.S. National Museum. In 1960 he returned to the United States at Atlanta, Georgia, and also visited Sao Paulo, Brasil. From November 1961 to March 1962 he visited Italy, France, Switzerland, and Spain and spent March and April of that year at the British Museum (Natural History). Next, on education business in 1964, he went to Puerto Rico and the United States again, visiting several states including California. He studied butterflies of the high Andes in Colombia, Ecuador and Perú, collecting and visiting museums during July and August of 1969. He returned to California in 1979 and in 1982 when he worked at the University of California at Davis and at the Oakland Museum. He traveled to Antarctica in 1980, to Florida and the Allyn Museum in September and October of 1984, then returned to California in 1988.

Don José also traveled extensively in Chile collecting insects, often with a busload of his students. He very much enjoyed having students about him. Pepe was very athletic in his youth, and held for a time the national championship in the long jump; he prized an action photograph of him in competition which he had hanging in his office. This interest in his fitness took him, whenever possible, to some of the numerous hot springs and bath resorts, or *termas*, that are scattered along the Andes and foothills of at least the northern two thirds of Chile. Many of his favorite collecting localities reflect his visits to such hot springs "for his health."

He was especially interested in Chilean butterflies and had hoped to complete a book on the Butterflies of Chile. This led to his collaboration with several northern Lepidopterists with whom he became acquainted over the years in connection with Chilean Nymphalidae, Satyridae, Pieridae, Lycaenidae and Hesperidae, e.g. T. G. Howarth, W. D. Field, A. M. Shapiro, L. D. Miller, K. Johnson, and me. Pepe had accumulated a large and valuable collection of Chilean Lepidoptera which was housed at the University. This collection was destroyed by deliberate burning during the campus riots by the Socialistas in 1973. Very little material survived the fire. He never got over the loss and never felt comfortable again about keeping valuable specimens at the University. He had gathered a small collection since then which he kept at his home. He was much concerned about conserving native species. He was interested in establishing a Butterfly House of native species, and wished to reintroduce to Cerro San Cristobal in Santiago larval food plants, nectar sources and native butterflies of Chile. He was working with several people in authority toward that goal.

There can be little doubt that Pepe was the dean of Lepidoptera in Chile; he knew the fauna extremely well and produced a number of students of Lepidoptera. His eye for discriminating species was acute as was his sense of similarities. Pepe was a strong believer in the reliability of genitalic characters in taxonomy and this led to spirited discussions. Art Shapiro tells of one such discussion where he ultimately challenged Pepe to a test; Shapiro would send him ten separated pierid abdomens with code numbers only and Pepe would report the identifications. Shapiro had included a couple of natural hybrids from Patagonia. He reports that Pepe got nine and a half correct. (He called a hybrid one of its presumptive parents.) Art has done this test with others and states that no one has ever come close to Pepe's record.

Pepe was a very good natured man who would unexpectedly burst into song. He had a refreshing sense of humor. He never felt comfortable with English and was wonderfully amused by his misadventures with the language. He delighted in the retelling of these misunderstandings and their consequences, told with much drama and expressive gesture. He was a proud man; proud of his family, his home and garden. He was proud too, of his accomplishments and the people he had met, and of his country. He loved fine wine and kept an extensive cellar of special vintages, a bottle of which was likely to appear at

the dinner table. He was fun to be around and had an infectious personality that made him many friends wherever he traveled. He will be remembered fondly and much missed by all those he touched.

My thanks for reminiscences or helpful suggestions to Art Shapiro, Lee Miller, and Jackie Miller. To Pepe's wife Ernesta, and his daughter Nieves Andredez, I am particularly grateful for generous help. I extend to them and their family my deepest sympathy.

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PUBLICATIONS OF JOSE HERRERA G.

1949

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1950

2. Dos géneros nuevos de nimfálidos para Chile. An. Univ. Catól. Chile 25(1):5-15

1952

3. Ausancia de dimorfismo sexual en *Colias flaveola* Blanchard. Rev. Chilena Entomol. 2:173-177.
4. La pesca con redes. Bol. Inst. Nac. 18(43):33-34, 1 fig. Santiago.

1953

5. La pesca de la albacora. Bol. Inst. Nac. 18(45):27-28. Santiago.

1954

6. Lepidópteros nuevos para Chile (Pieridae). Rev. Chilena Entomol. 3:140-147, 12 figs.
7. La enseñanza de la zoología sistemática en el liceo. Ministerio de Educación Pública. 58 pp., 13 pls.
8. Curso de Zoología (Artrópodos, Vermes y Moluscos). 2 vols. Editorial Universitaria, Santiago.
9. Herrera, J. & O. Palma. Los principios fundamentales de la biología (translation of English). Públ. Minister. Ed. Santiago.

1955

10. Curso teórico-práctico de entomología. Editorial Universitaria, 324 pp., 93 pls. Santiago.

1956

11. Herrera, J., M. Etcheverry & A. Carrasco. Los Odonatos de Chile. Rev. Universitar. Univ. Catól. Chile 40 & 41(1):63-88, 33 figs. Santiago.

1957

12. Notas etnoentomológicas del pueblo de Putra. Notas Cent. Estud. Antropológicos No. 1:9. Univ. Chile.

13. Herrera, J., M. Etcheverry & C. Hochleitner. Los Pyrginae de Chile (Hesperiidae). Rev. Chilena Entomol. 5:143-182, 1 pl., figs. 1-19.
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1958

15. Las puebas del bachillerato. Editorial Universitaria Santiago.
16. Herrera, J., M. Etcheverry & M. Barrientos. Los Nymphalidae Chilenos. An. Univ. Chile 116(111):237-268, 2 pls., figs. 1-51. Santiago.
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1959

18. Herrera, J. & W. Field. A revision of the butterfly genera *Theochila* and *Tatochila* (Lepidoptera, Pieridae). Proc. U.S. Natl. Mus. 108:467-514, 93 figs.

1960

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20. Papilionidae de Chile. Rev. Universitar. Univ. Catól. Chile. 44 & 45:153-155. Santiago.
21. El concepto de especie. Rev. Universitar. Univ. Catól. Chile: 44 & 45:157-163. Santiago.

1961

22. Plan de integración educacional de Arica. Ministerio de Educación Pública. 50 pp., 8 pls.

1963

23. Curso teórico-práctico de entomología, 2nd ed. Editorial Universitaria, Santiago.

1964

24. Etcheverry, M., J. Herrera & L. Russel. Principios de biología moderna de D. Marsland. Editorial Universitaria. 616 pp., 27 tabs., 446 figs. (translation of English of 3rd ed.)

1965

25. *Etcheverrius* y *Palmaris*, nuevos géneros de Satyridae Andinos (Lepidoptera). Publ. Cent. Estud. Entomol. No. 7; 57-73, figs. 1-26, 34-39, 59-63. Santiago.
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27. Herrera, J. & M. Etcheverry. *Stuardosatyrus* nuevo género de Satyridae y revalidación de la especie *williamsianus*, Bulter, 1868. Publ. Cent. Estud. Entomol. No. 7:74-77, figs. 27-33, 50-58. Santiago.

1966

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29. Ejemplar hermafrodita de *Quilaphoetus janiroides* Blanchard (Lepidoptera, Satyridae). Publ. Cent. Estud. Entomol. 8:127-133, 3 pls. Santiago.
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1970

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1971

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1972

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35. Curso teórico-práctico de entomología. 3rd ed., 365 pp., 50 pls. Editorial Universitaria, Santiago.

1974

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1977

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38. Field, W. & J. Herrera. The pierid butterflies of the genera *Hypsohila* Ureta, *Phulia* Herrich-Schäffer, *Infraphulia* Field, *Pierphulia* Field and *Piercolias* Staudinger. Smithsonian Contrib. Zool. No. 232:1-64, 5 maps, 198 figs.

1981

39. Biología de *Cynthia carye* Hübner 1812, especie críptica de *Cynthia annabella* Field 1971 (Lepidoptera). IV Congreso Latinoamer. de Entomol. Actas del Congreso.

1982

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CONTENTS

TEMPORAL CHANGES IN ABUNDANCE OF TWO LYCAENID BUTTERFLIES (LYCAENIDAE) IN RELATION TO ADULT FOOD RESOURCES. <i>C. J. Hill</i>	173
GENITALIC CHARACTERIZATION, ENLARGEMENT, AND REASSOCIATION OF THE NEOTROPICAL HESPERIINE GENUS <i>HALOTUS</i> (HESPERIIDAE). <i>John M. Burns</i>	182
FOODPLANT SPECIFICITY AND BIOLOGY OF <i>OIDAEMATOPHORUS BALANOTES</i> (PTEROPHORIDAE): A NORTH AMERICAN MOTH INTRODUCED INTO AUSTRALIA FOR THE BIOLOGICAL CONTROL OF <i>BACCHARIS HALIMIFOLIA</i> . <i>W. A. Palmer and W. H. Haseler</i>	195
BIOLOGY OF EPIPHYLL FEEDING BUTTERFLIES IN A NIGERIAN COLA FOREST (LYCAENIDAE: LIPTENINAE). <i>Curtis J. Callaghan</i>	203
POTENTIAL FOR THE NON-INVASIVE STUDY OF INSECT HEART FUNCTION WITH A DOPPLER CRYSTAL SYSTEM. <i>Jon D. Turner</i>	215
TWO NEW SPECIES OF MOTHS (NOCTUIDAE: ACRONICTINAE, CUCULLIINAE) FROM MIDLAND UNITED STATES. <i>Charles V. Covell Jr. and Eric H. Metzler</i>	220
GENERAL NOTES	
Parasitoid induced mortality in the eggs of the endangered giant swallowtail butterfly <i>Papilio homerus</i> (Papilionidae). <i>Eric Garraway and Audette J. A. Bailey</i>	233
World distribution of the <i>Vanessa cardui</i> group (Nymphalidae). <i>Oakley Shields</i>	235
Notes on the type of <i>Papilio cresphontes</i> ab. "maxwelli" (Papilionidae). <i>John V. Calhoun</i>	238
BOOK REVIEWS	
The Nepticulidae and Opostegidae (Lepidoptera) of north west Europe. <i>Donald R. Davis</i>	240
Distribution of butterflies in New Mexico (Lepidoptera: Hesperioidea and Papilionoidea). <i>George T. Austin</i>	241
Simon & Schuster's guide to butterflies and moths. <i>Lawrence F. Gall</i>	242
Larvae of owlet moths (Noctuidae): Biology, morphology, and classification. <i>Thomas D. Eichlin</i>	243
Discover butterflies! An activity book for families, students, and teachers. <i>Thomas C. Emmel</i>	244
Biología y morfología de las Orugas: Lepidoptera, Vol. 6: Syssphingidae—Saturniidae—Endromidae—Lasiocampidae—Drepanidae—Thyatiridae—Notodontidae—Hypsidae. <i>Richard S. Peigler</i>	246
OBITUARY	
José Valentín Herrera González. <i>C. Don MacNeill</i>	248

Volume 46

1992

Number 4

ISSN 0024-0966

JOURNAL

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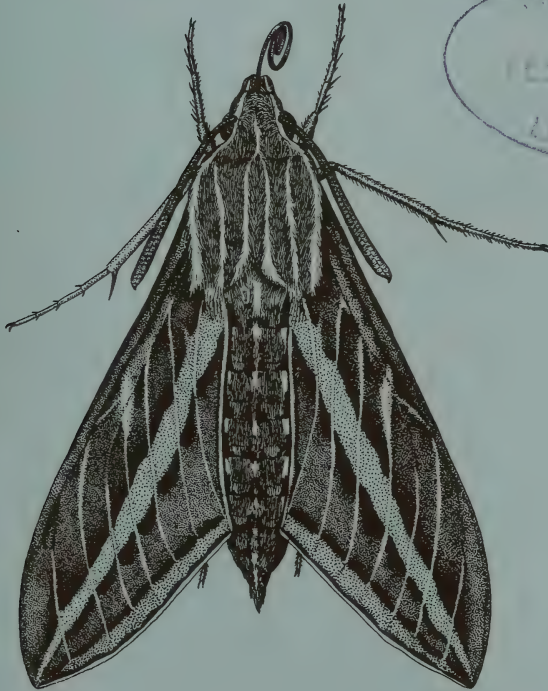
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Cover illustration: The white-lined sphinx moth, *Hyles lineata* (Fab.) (Sphingidae), is the most common and widespread member of the family in North America. Larvae feed on a wide variety of dicotyledenous plants in several families, including Rosaceae, Solanaceae, Onagraceae, Portulacaceae, and Nyctaginaceae. Submitted by Callie Mack, 8529 Jackie Drive, San Diego, California 92119 U.S.A.

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GRADIENTS IN BUTTERFLY SPECIES DIVERSITY IN AN URBAN AREA IN BRAZIL

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ABSTRACT. The diversity (Shannon-Weaver) of butterflies throughout the urbanized area of Porto Alegre, Brazil, was analyzed using 109 sampling areas within three characteristic zones of urbanization: buildings (B), houses and buildings (HB), and houses (H). Highest diversity was found in the periphery of the houses zone (H) one to two kilometers beyond the perimeter of the houses and buildings zone (HB). From zone H to zone HB we observed a significant decrease in diversity and a small overlap in community composition (Renkonen's PS). From zone HB to a central zone of buildings (B), there was a relatively small change in community composition demonstrated by statistically similar diversity indices and a high species similarity. These findings suggest the existence of two macrohabitats for butterflies in the city: 1) B + HB and 2) H. Samples from areas within the same urbanized zone showed the highest degree of similarity. Diversity decreased in the B + HB macrohabitat mainly owing to a reduction in species richness (S). Biotic and abiotic factors that may be involved in this reduction are discussed. For late spring and midsummer samples, nearly 50% of the variation in diversity was explained by vegetation cover and distance from the city center. This value rises to 63% for the total diversity and 70% for the log transformation of species richness. These high proportions emphasize the importance of regional urban environmental conditions for butterfly diversity. In the winter, only vegetation cover presented a partial regression coefficient that was significant, accounting for less than 20% of the variation in diversity. Also, a scattered distribution of areas with high butterfly diversity associated with high vegetation cover was observed during the winter.

Additional key words: urban ecology, urban Lepidoptera, insect diversity, man-made habitats, community structure.

The structure and diversity of biotic communities within urban environments are important for theoretical and practical reasons. Urban biotas can be studied from a genetic and evolutionary perspective, as

exemplified by Bishop and Cook (1981), or from an ecological perspective as demonstrated by Ruszczyk (1987). The ecological consequences of urbanization for particular groups of plants and animals can indicate the degree of disturbance of such environments and may be useful in developing strategies for conservation.

In a previous study, Ruszczyk (1987) presented maps of the distributions of 29 species of butterflies within the urbanized area of Porto Alegre, Brazil. Species exhibited variable rates of decline toward the highly-developed urban center. The border between a predominantly house-occupied zone (H) and a zone of houses and buildings in equal proportions (HB) was found to be the main area of transition for the urban fauna, acting as an ecological barrier for species typically associated with woods or natural fields. Species that are associated with open areas, that are highly vagile, and that have larvae that utilize both native and exotic cultivated plants were dominant in the city. Distance of the sampling areas from the center of the city was found to be a better predictor of butterfly numbers than average elevation or vegetation cover.

In this study we further analyzed butterfly diversity for 109 sampling points. We also investigated factors influencing spatial patterns of diversity and species richness within the city as well as the similarities in the structure of butterfly communities in regions within different levels of urbanization.

MATERIALS AND METHODS

Study area. Porto Alegre is a large urban area in Rio Grande do Sul in southern Brazil (30°02'S 51°14'W; 1,000,000 inhabitants). It has a temperate-subtropical climate with high humidity and moderately high temperatures in the summer. Mean annual temperature is 13.8°C, and average annual rainfall is 1322 mm. Three characteristic zones of urbanization were identified (Ruszczyk 1987): a buildings zone (B) with buildings more than four stories high and vegetation cover below 20%; a houses-and-buildings zone (HB) with equal proportions of lower buildings and houses and vegetation cover between 20 and 40%; and a houses zone (H) with mostly houses but including open areas within the city, and vegetation above 40% (Fig. 1a). The urbanized zones illustrated in Fig. 1A were simplified by drawing tangential lines to the borders of the different urbanized zones (Fig. 1b).

Data collection. A 1 km grid was superimposed on the map of the urbanized zones resulting in 109 contiguous sample areas within the city. Sampling areas (SAs) were arbitrarily delineated as 600 m diameter circles (Fig. 1b). SAs were surveyed for butterflies during three sampling periods: November–December 1980, March–April 1981, and June–July

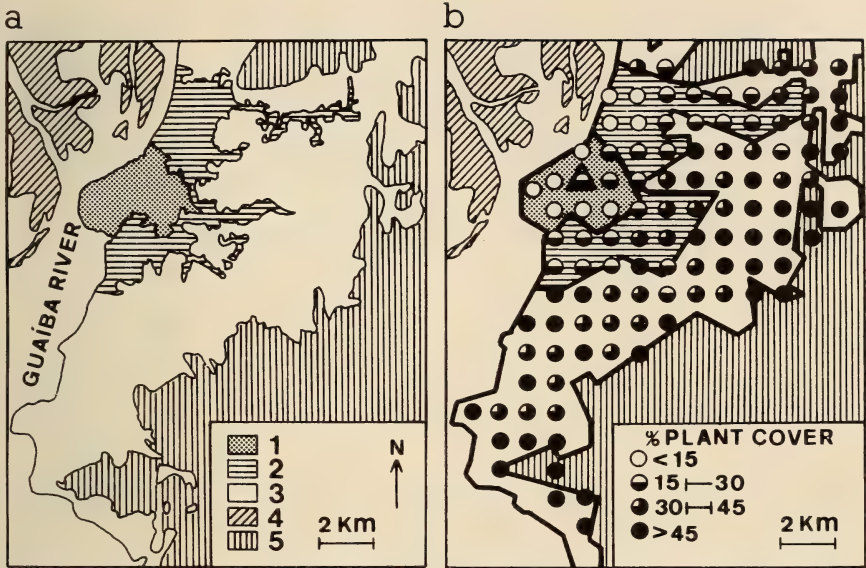


FIG. 1. Urbanized zones of Porto Alegre in 1981 (a), and distribution of sampling areas in a simplified map (b). The triangle in Fig. 1b indicates the center of the buildings zone. 1, buildings zone; 2, houses-and-buildings zone; 3, houses zone; 4, marshes; 5, extraurban area.

1981. Each SA was sampled sequentially, five SAs per day between 1000–1600 h. SAs were censused by walking continually along the streets and recording the number of each butterfly species observed during a 45 minute period (see Ruszczyk 1987 for further details of the sampling program and study area). The distance between each SA and the SA at the center of the building zone (marked with a triangle in Fig. 1b) was considered the “distance from the city center.” The average elevation of each SA was calculated as the arithmetic mean of its highest and lowest points.

Data analysis. The Shannon-Weaver index (Margalef 1958, Lloyd & Ghellardi 1964, Pielou 1966) was used to calculate diversity (H') for each SA. The SAs were grouped in three sets related to the three urbanized zones. The differences between the calculated indices for these sets were compared using a t -test modification proposed by Poole (1974) for evaluating diversity calculations. In addition, a one-way analysis of variance was applied to the three sampling periods (Nov–Dec/80; Mar–Apr/81; Jun–Jul/81) disregarding the zones, to test the effects of seasonality on mean diversity. The degree of similarity among samples was measured using Renkonen’s Percentage of Similarity (PS). For this analysis, SAs were combined into 11 regions with similar area within a single urbanized zone. This reduced the area matrix from 109

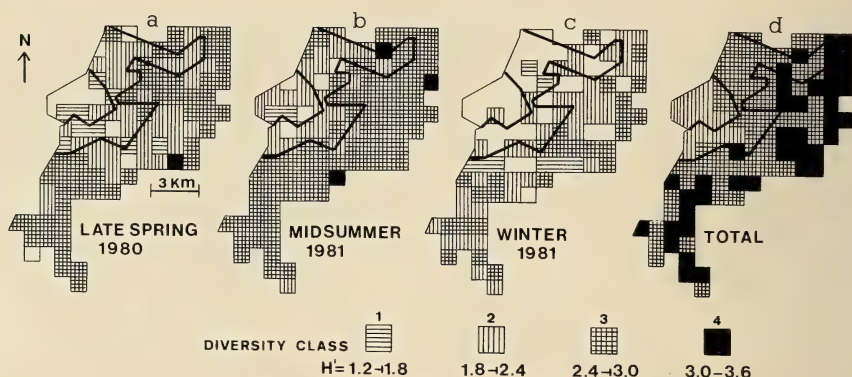


FIG. 2. Diversity index (Shannon-Weaver) of butterfly communities in the urbanized zones of Porto Alegre. Clear areas indicate less than 12 individuals recorded; bold lines separate urbanization zones (see Fig. 1b).

sampling points to 11 contiguous areas and permitted detection of patterns among city regions rather than local faunal similarities. Grouping of regions in the principal matrix followed the simple average method (Sneath & Sokal 1973). The relative influence of 1) percentage of area covered by vegetation, 2) distance from the city center, and 3) mean elevation of each SA on butterfly diversity and on the total number of species was calculated using multiple regression. The explained variation (R^2) of the dependent variables was partitioned into components attributed to each independent variable following the standard regression method (Kim & Kohout 1975).

RESULTS

Highest diversity values were found in zone H, typically one to two km beyond the perimeter of zone HB (Fig. 2). In late spring and midsummer (Figs. 2a & 2b), patterns of diversity were strongly correlated with urbanized zones—zone H typically had diversity values greater than $H' = 2.4$ (Fig. 2, diversity class no. 3) and zone HB had lower values. During winter (Fig. 2c) there was greater variability in the diversity indices. However, the peripheral area of the houses zone (H) continued to support greater diversity.

Papilionini and Heliconiini, two tribes that are abundant in the city, showed the same tendencies as described above (Fig. 3). A considerable decrease in the number of species in these two groups was observed at the border between zones H and HB. In zone B the number of species was fairly constant—one or two. The highest number of species was recorded in the periphery of zone H. In the winter, the number of species decreased greatly, especially in zones B and HB (Fig. 3).

Multiple regression of diversity (using pooled seasonal data) with the



FIG. 3. Number of species of Papilionini (a) and Heliconiini (b) in the urbanized zones of Porto Alegre. Each three-column group indicates the number of species recorded (from left to right) in late spring 1980, midsummer 1981 and winter 1981.

number of species and species evenness showed a greater interaction with the number of species in the explained variance of diversity ($R^2 = 0.90$) than with the species evenness ($R^2 = 0.10$). The standardized regression coefficient (variables transformed to have unit variance allowing the comparison of variables measured in different units) of the number of species (0.98) was nearly three times greater than for evenness (0.35), indicating that diversity decreased in zones B and HB mainly due to the reduction in the number of species in these zones. Diversity indices for the entire zone H (summation of SA data) were significantly higher than for zones HB and B. On the other hand, the indices for zone HB and B were not statistically different (Table 1).

TABLE 1. Diversity of butterflies in three urbanized zones of Porto Alegre. The lines indicate indices that were statistically similar ($P < 0.05$). Differences between indices were compared using a *t*-test modification proposed by Poole (1974).

Sample	Urbanized zone		
	Buildings	Houses-and-buildings	Houses
Late spring, 1980	2.5414	3.0304	3.4785
Midsummer, 1981	2.6344	3.0145	3.3108
Total	2.9277	3.2251	3.4873

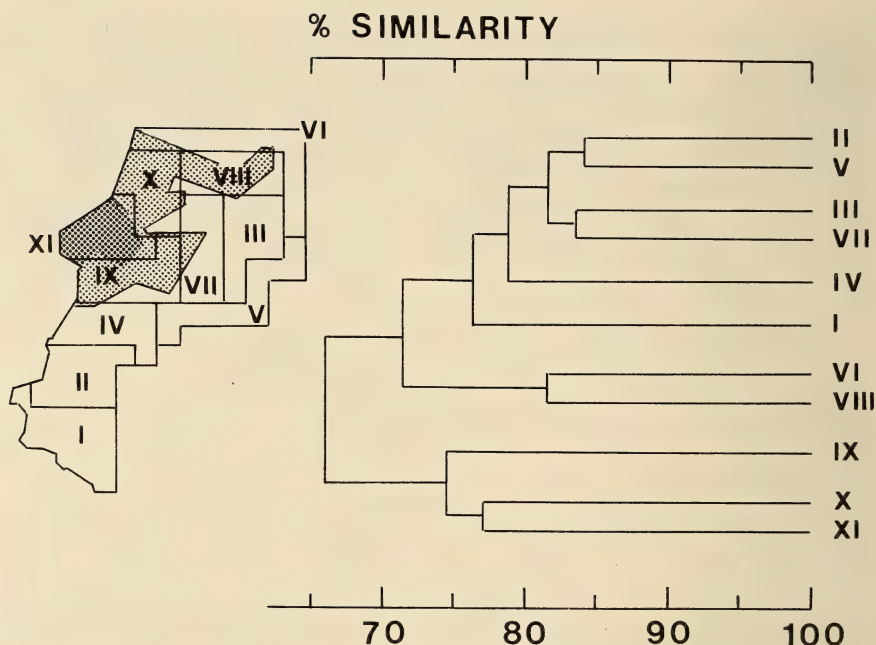


FIG. 4. Similarity (Renkonen's index) in the structure of butterfly communities of regions within the city of Porto Alegre. I to VII, houses zone; VIII to X, houses-and-buildings zone; XI, buildings zone.

Figure 4 illustrates the results of PS calculations. Two distinct clusters of regions are evident: 1) regions I to VIII, all but the last of which are located in zone H, with a high internal PS; and 2) regions IX and X in zone HB and region XI in zone B, with a comparatively low internal PS.

Standardized regression coefficients of distance from the city center and vegetation cover with diversity and the log number of species, were similar; but distance had a slightly greater value (Table 2). In midsummer, distance was almost twice that of vegetation cover. In the winter, vegetation cover showed a significant partial regression coefficient with diversity, though accounting for less than 20% of the explained variation in diversity. In late spring and midsummer, about 50% of the variation in diversity was explained by vegetation cover and distance from the city center. This value increased to 63% for the total diversity and 70% for the log number of species. These high proportions demonstrate that such variables are important determinants of butterfly community structure in Porto Alegre. However, the contribution of each variable alone was, in general, less than 11%. More than 30% of the variation was due to the interaction of vegetation cover and distance, whose effects on butterfly diversity and species number was neither indepen-

TABLE 2. Decomposition of the explained variation in butterfly diversity (Shannon-Weaver index) in three sampling periods, and total number of species ($\ln S$) into components attributed to the independent variables percentage of area covered by vegetation of the sampled area (X_1) and distance from the city center (X_2). Standardized regression coefficients in parentheses. Angular transformation was used for X_1 and logarithmic for X_2 .

Dependent variable (Y)	Proportion of variation explained by X_1 and X_2 (R^2)	Increment due to vegetation cover (X_1)	Increment due to distance from the city center (X_2)	Not attributed to either X_1 or X_2 alone
Diversity				
Late Spring 1980	0.456	0.058 (0.341)	0.075 (0.390)	0.323
Midsummer 1981	0.489	0.043 (0.289)	0.108 (0.464)	0.338
Winter 1981	0.171	0.171 (0.413)	—	—
Total 1980-1981	0.630	0.078 (0.394)	0.107 (0.465)	0.445
Log no species	0.703	0.096 (0.440)	0.109 (0.467)	0.498

(—), partial regression coefficient not significant after the inclusion of the variable in the multiple regression equation.

dent nor additive (Table 2). The biological mechanism underlying the strong association between these two variables affecting butterfly diversity and species number cannot be inferred from these data alone. Average elevation was excluded from this analysis because in the presence of the other variables its partial regression coefficient was not significant.

A marked seasonality in diversity was observed in Porto Alegre (Fig. 5), with mean diversity of each sampling period significantly different even when the zone data were pooled (Table 3).

DISCUSSION

The buildings zone (B) did not form a subset isolated from the houses-and-buildings zone (HB) (Fig. 4), and the diversity indices for these zones were statistically similar (Table 1) revealing their similar butterfly

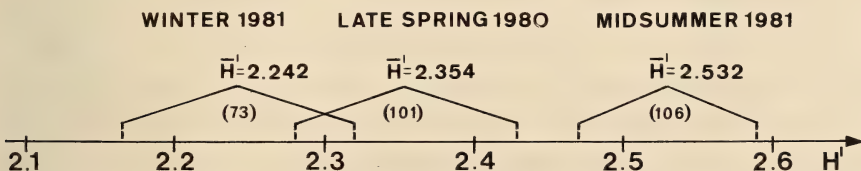


FIG. 5. Confidence intervals ($P = 0.95$) of the means of butterfly diversity in urban Porto Alegre during three sampling periods. Number of sampled areas between parentheses.

TABLE 3. Results of the one-way ANOVA for mean diversity in three sampling periods, independently of urbanized zone. H_1 = Late Spring 1980; H_2 = Midsummer 1981, H_3 = Winter 1981.

Source	SS	DF	MS	F	P
Between	3.7050	2	1.8525	15.47	<0.001
($H_1 \cdot H_2$) vs. H_3	2.1274	1	2.1274	17.77	<0.001
H_1 vs. H_2	1.5776	1	1.5776	13.18	<0.001
Within	31.9676	267	0.1197		
Total	35.673	269			

community structure. Zone B can be seen as a portion of the zone B + HB macrohabitat where environmental conditions are more harsh for butterflies, but without divergence of the typical community of butterflies of zone HB. In this community (B), several species of butterflies that are relatively abundant in zone H, are scarce or absent. These include woodland species, such as *Heliconius erato phyllis* (Fabricius), *Eunica margarita* (Godart), *Adelpha* spp. (Nymphalidae), *Battus* spp., *Parides* spp. (Papilionidae); Nymphalidae that feed on fruit and sap (*Hamadryas* spp., *Anaea* spp.); species characteristic of fields, such as *Colias lesbia pyrrhothea* (Huebner), *Eurema* spp. (Pieridae), *Euryades corethrus* (Boisduval) (Papilionidae), *Junonia evarete* (Cramer), *Vanessa* spp. (Nymphalidae); and some eurytopic species, such as *Dryas iulia* (Fabricius), *Anartia amathea* (Eschscholtz) (Nymphalidae), *Papilio hectorides* Esper, and *Papilio astyalus* Latreille (Papilionidae). All species found in zones B and HB also were observed in zone H. These species [e.g., *Papilio scamander* Boisduval, *Papilio anchisiades capys* Huebner (Papilionidae), *Ascia monuste orseis* (Latreille), *Tatochila autodice* (Huebner), *Phoebis philea* (Johansson) (Pieridae), and *Dryas iulia*] are the most widespread in the city, attaining high densities in all urbanized zones (Ruszczyk 1987). The impoverishment of the butterfly community in the B + HB urbanized zone is likely the result of the considerable environmental disturbance in this area as compared to zone H. Abiotic and biotic factors are harsher in zone B + HB than in zone H. Abiotic factors include the following: a) dry and strongly illuminated habitat (e.g., all watercourses are channelized, there are few shaded areas, and there is high sunlight penetration to the ground); b) greater air pollution owing to traffic; c) habitat disturbance from intense human movement and traffic; and d) streets and sidewalks completely paved and a large percentage of the area occupied by buildings, diminishing the resources at the soil surface. Biotic factors include the following: a) lower percentage of area covered by vegetation which acts to decrease diversity within these zones by lowering primary productivity (Connell & Orias 1964), and the accentuated fragmentation of the vegetation probably reduces colonization

and dispersion of butterflies; b) relative homogeneity of vegetation (in zones B and HB relicts of native vegetation were not observed, and many plants that are common in outlying areas were very scarce, giving a qualitative decrease in nectar sources and potential food plants for larvae); and c) smaller contribution of elements of the extraurban fauna (zones B and HB probably have small participation of the transitory species from peripheral areas than zone H, which is in direct contact with remnants of natural habitats).

The formation of butterfly diversity gradients in the city is in contrast to the results obtained in studies of soil arthropods, which seem to respond more to local (soil) variables than to urban environmental gradients (Kühnelt 1955, Topp 1972, Lussenhop 1973, Maurer 1974). More recently, Klausnitzer and Richter (1983) demonstrated the presence of an urban gradient for carabids in the city of Leipzig, Germany. As for butterflies, the distance from the center of the city showed a greater influence on diversity than vegetation cover or mean elevation, emphasizing the importance of macrohabitat conditions for these insects.

Distance correlated well with butterfly abundance (Ruszczyk 1987) and diversity (present paper) in Porto Alegre, Brazil, probably because many parameters that are important for butterflies are radially dispersed in the city due to the radial pattern of the urbanized zones.

The non-significance of the partial regression coefficient of distance from the city center during winter, and the island character of the class distribution of diversity (Fig. 2c), suggest that winter butterfly diversity depends on qualitative variables such as presence of habitat refugia. When compared to other zones, zone H showed greater possibilities for the presence of such refugium. In the winter, a higher diversity was scattered among 26 SAs, all but one of which was situated in zone H; 19 of these SAs possess vegetation cover greater than 45%. This provides evidence of the biotic value of urban vegetation, and suggests that fragments of habitat within the urbanized areas, especially urban forest fragments (Rodrigues et al. 1992), may perform a vital role in maintaining local biodiversity.

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A NEW TEXAS CLEARWING MOTH (SESIIDAE: SESIINAE)

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ABSTRACT. A new species of clearwing moth, *Carmenta flaschkai*, from Fort Davis, Texas is described. The male genitalia are illustrated.

Additional key words: *Carmenta flaschkai*, *C. verecunda*, *Synanthedon canadensis*, sex attractant, couplet.

Since the recent publication of a revision of North American Sesiidae (Eichlin & Duckworth 1988), a small series of male clearwing moths from Fort Davis, Texas were sent to me for identification. Generally, they resemble specimens of *Carmenta verecunda* (Hy. Edwards). However, they differ in certain color patterns and basic structural details of the genitalia.

Carmenta flaschkai, Eichlin, new species (Figs. 1–3)

Description (male only, Figs. 1 & 2). Head and vertex brown-black, overlapping front; front gray-black or white, laterally white, white at base of antennae; occipital fringe dorsally mixed pale yellow and brown-black, laterally white; antennae brown-black; labial palpus thickened, somewhat roughened ventrally, white with brown-black laterally and apically. Thorax brown-black, pale yellow to white in patch beneath wing and in tuft above and behind wing base, very narrow orange, subdorsal, longitudinal stripe. Abdomen brown-black, dorsally with narrow, pale yellow or white bands on posterior of segments 4, 6 and 7; ventrally strongly banded pale yellow or white on 4–7, white variously on other segments; anal tuft dorsally brown-black with yellow-orange medially, ventrally yellow-orange. Legs brown-black with white on forecoxa; tibiae white on proximal half dorsally and laterally, with some white tufted distally. Fore wing with hyaline areas in cell and distally mostly covered with opaque white scales, margins and discal spot brown-black, apical margin variously broad and suffuse, pale orange on posterior margin and on posterior edge of cell. Hindwing hyaline but with somewhat cloudy (milky) translucence. Wing length 8–9 mm (one specimen 7 mm). Genitalia (Fig. 3) with saccus elongate, more than one third length of valva; scopula androconialis long, slightly longer than saccus.

Types. Holotype, male, (USNM): "TX, Jeff Davis Co., Ft. Davis, 11.IX.91, lg. D. Marqua, 99:1."

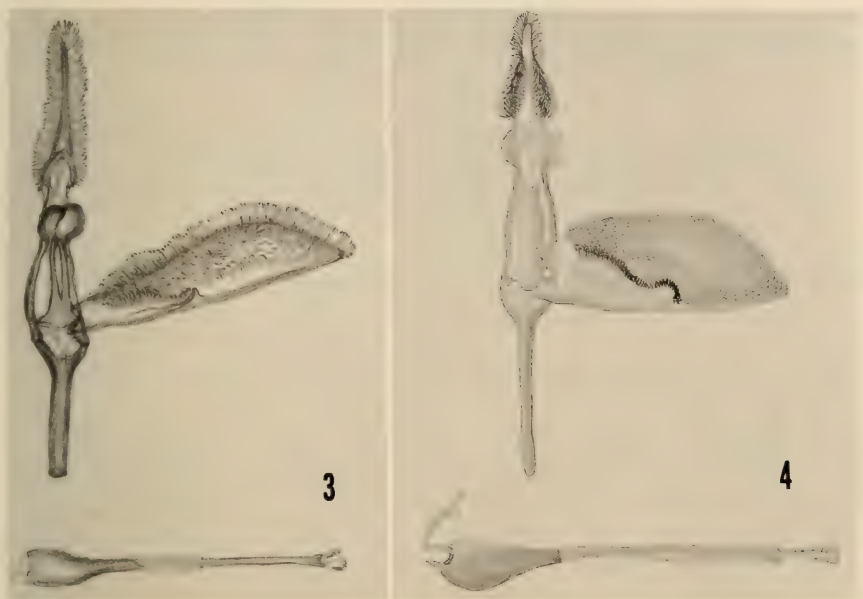
Paratypes, 15 males, (USNM, CDFA, CAS, Flaschka): (15) same as holotype except: (1) Genitalia Slide, CDFA #811, by S. A. Kinnee; (1) 29.VIII.91, L-103; (1) 9.IX.91; (1) 15.IX.91; (1) 1.X.91; (2) 2.X.91; (3) 5.X.91; (5) 14.X.91 (1 with Genitalia Slide, CDFA #816).

Distribution. Known only from the type locality: Fort Davis, Jeff Davis Co., Texas.

Discussion. *Carmenta flaschkai* is similar in appearance to *C. verecunda*, in particular the form described as *hirsuta* Englehardt. The latter form also was described from the same general area—Davis Mountains, Texas. However, *C. flaschkai* has pale orange near the



FIGS. 1-2. Male, *Carmenta flaschkai* (wing length 8 mm). 1, Dorsal view. 2, Ventral view.



FIGS. 3-4. Male genitalia (aedeagus detached). 3, *Carmentis flaschkai*. 4, *C. verecunda*.

forewing base extending distally on Cu and the anal margin; additionally, the male genitalia has the scopula androconialis elongated (Fig. 3), this structure being much reduced on *C. verecunda* (Fig. 4).

Because of the orange scaling on the anal tuft, especially ventrally, *C. flaschkai* will not key out with *C. verecunda* (Eichlin & Duckworth 1988:69, couplet 8) but runs to couplet 10 with *Synanthedon canadensis* Duckworth and Eichlin. Hence, an additional couplet is required:

- 10b. Antenna powdered with pale yellow; labial palpus with yellow-orange ventrally and mesally *S. canadensis*
 - Antenna without yellow; labial palpus with white not yellow-orange .. *C. flaschkai*

The type series was collected with the aid of a chemical sex attractant consisting of a mixture (99:1) of (Z, Z/E, Z) 3,13-octadecadiene-1-ol acetate (ODDA).

This species is named for Hermann Flaschka, of Decatur, Georgia, in recognition of the contributions he has made to my studies of the Sesiidae through sharing his specimens, data, and collecting experiences.

ACKNOWLEDGMENTS

I thank Dave Marqua for collecting the type series and Hermann Flaschka for making the specimens available to me for examination. Technical expertise was provided by my

assistant Scott Kinnee. The drawing of the genitalia of *C. verecunda* was originally rendered by Laura Keller (Duckworth & Eichlin 1978).

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HOLARCTIC DISTRIBUTION OF
CHORISTONEURA ALBANIANA (WALKER), WITH
NEW SYNONYMY (TORTRICIDAE)

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ABSTRACT. *Choristoneura albaniana* (Walker) occurring in the northern regions of North America, and *C. lapponana* (Tengström) occurring in northern Europe and Siberia, are conspecific; the name *C. albaniana* has priority. This new synonymy helps determine the holarctic range of this species.

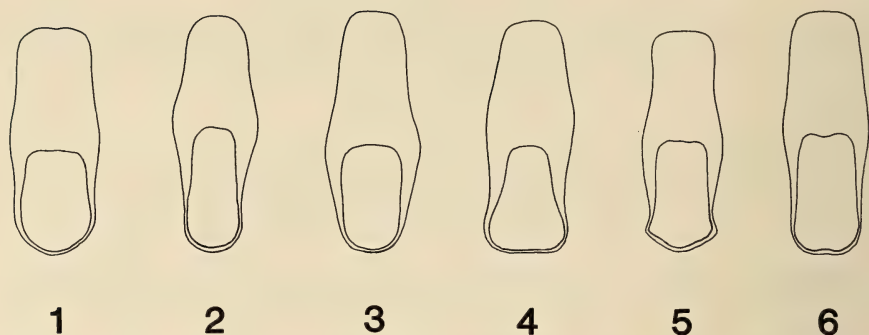
Additional key words: *Choristoneura lapponana*, transcontinental, male genitalia.

Choristoneura Lederer is a Holarctic genus. *Choristoneura fumiferana* (Clemens), *C. rosaceana* (Harris), and *C. conflictana* (Walker) of the Nearctic, and *C. diversana* (Hübner), *C. murinana* (Hübner), and *C. lafauryana* (Ragonot) of the Palaearctic, are widespread and transcontinental, but none has been recorded in both regions (Freeman 1958, Powell 1983, Kloet & Hincks 1972, Varis et al. 1987).

Choristoneura albaniana (Walker), described from a specimen collected in St. Martin's Falls, Ontario, is a transcontinental species that has been recorded in northern parts of North America, i.e., Alaska, Yukon, Northwest Territories, northern Manitoba, western Ontario, northern Quebec, and Labrador to Newfoundland. A southern record is represented by two specimens from Mt. Evans, Colorado. A specimen collected from Black Sturgeon Lake, Ontario, has a note indicating pin cherry, *Prunus pensylvanica* L. (Rosaceae) as a host plant.

Choristoneura lapponana (Tengström), described from Finland, has been recorded in northern parts of the Palaearctic region, including Sweden, Finland, Ural, Trans-Baikal, Amur, and along the taiga zone in the Siberian region (Kennel 1929, Kuznetsov 1973, 1978, Varis et al. 1987), and in Yukon, Canada (Kuznetsov & Mikkola 1991). A food plant has not been identified positively for this species; larvae were reportedly found on larch (Kuznetsov 1978), but this record requires confirmation.

Study of the male genitalia of *C. albaniana* from North America and *C. lapponana* from Finland (Dang 1992) revealed that the structures of these two species are similar in every comparable aspect. The characteristic longitudinal split, connecting with the apical opening of the aedeagus, is distinctly shifted laterally to the right side, whereas in other *Choristoneura* species it is dorsally located; the apical spine of the aedeagus is vestigial. The uncus is small with a convex or truncate apex, and a distinctly widened midportion (Figs. 1-6). Further study of the wings of *C. albaniana* and *C. lapponana*, which exhibit similar and



FIGS. 1-6. Ventral view of unci of *Choristoneura albaniana* from various localities in North America and Europe: **1**, Black Sturgeon L., Ontario, Canada; **2**, Bradore Bay, Quebec, Canada; **3**, Cameron Bay, N.W.T., Canada; **4**, Doolittle Range, Mt. Evans, Colorado, USA; **5**, Enontekio Karesuanto, Finland; **6**, Kilpisjärvi, Finland.

consistent colors and patterns (Figs. 7-10), prompts the present review of their taxonomic status. The shade of color of the forewing varies slightly from specimen to specimen. The ground color of the forewing varies from beige to brownish yellow; the oblique faciae vary from reddish brown to dark brick brown. Most specimens from North America have paler hind wings; a few have the same color as those from northern Europe. The different shades of color likely represent individual variation. On the basis of the overall morphological similarity, it is concluded that *C. lapponana* and *C. albaniana* are conspecific; the name *C. albaniana* has priority. Consequently, *C. albaniana* represents the only *Choristoneura* species recorded across the Holarctic region.

Choristoneura albaniana (Walker)
(Figs. 1-10)

Teras albaniana Walker, 1863:288.

Choristoneura albaniana, Freeman 1958:38; Powell 1983:40; Dang 1992:19.

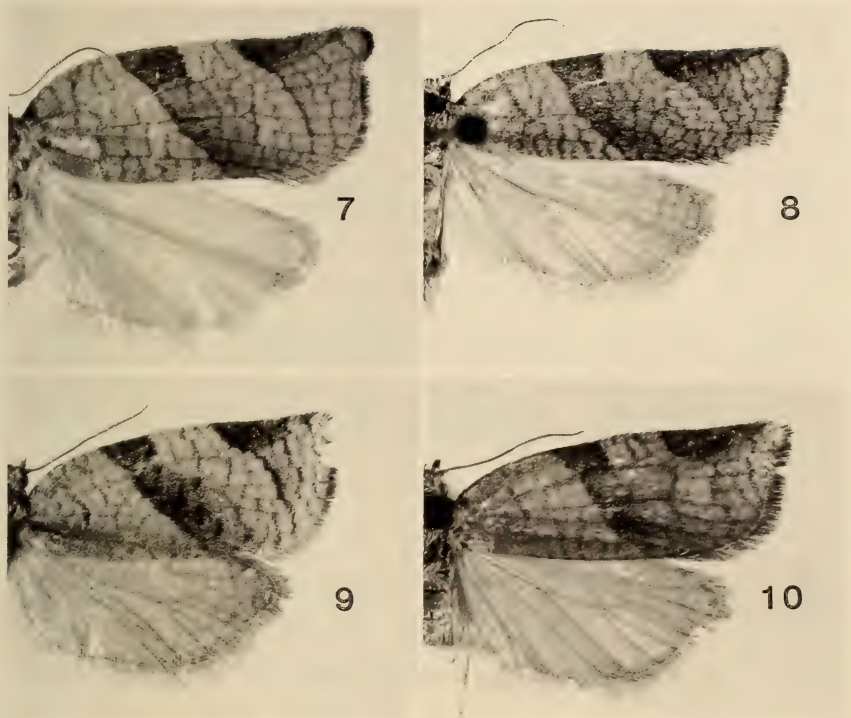
Tortrix lapponana Tengström 1869:359. **New Synonymy.**

Dichelia Lapponana (sic), Rebel 1901:85.

Epagoge lapponana, Kennel 1929:112; Benander 1950:25.

Choristoneura lapponana, Obraztsov 1955:203; Kuznetsov 1973:77, 1978:348; Varis et al. 1987:64; Dang 1992:19.

The synonymy proposed is based on the examination of two males and one female of *C. lapponana* from the type locality (Karesuanto, Finland) and several specimens from nearby areas and the holotype of *C. albaniana* in The Natural History Museum, London, England, as well as a number of specimens of *C. albaniana* from various localities across North America. The holotype of *C. lapponana*, which was not examined in the present study, is in the Zoological Museum, University of Helsinki, Finland.



FIGS. 7-10. Wing patterns of *Choristoneura albaniana* from various localities in North America and Europe: 7, Churchill, Manitoba, Canada; 8, Anchorage, Alaska, USA; 9, Enontekiö Karesuanto, Finland; 10, Kilpisjärvi, Finland.

Material studied. The number in parentheses immediately after the number of specimens studied indicates the number of male genitalia examined. CANADA: Newfoundland: Labrador, Hopedale, 12.VII.1927, 24.VII.1934, 26.VII.1935 (W. W. Perrett), 3 ♂♂ (1). Quebec: Indian House Lake, 11.VII.1954 (R. Coyles), 2 ♂♂ (1), and 12.VII.1954 (W. R. Richards), 2 adults without abdomen; Bradore Bay, 21 and 26.VII.1929 (W. J. Brown), 1 ♂ (1), 1 ♀; Knob Lake, 19.VII.1948, 16.VIII.1948 (E. Munroe), 1 ♂ and 1 ♀; Mt. Lyall, 1500', VII.1933 (W. J. Brown), 1 ♂ and 1 ♀. Ontario: St. Martin's Falls (HOLOTYPE ♂) (1), BMNH, Black Sturgeon Lake, VI.1961-VI.1964 (Light Trap), 19 ♂♂ (4); Moose Factory, 21.VI.1949 (D. F. Hardwick), 2 ♀♀. Manitoba: Churchill, 4.VII.1937 (W. J. Brown), 1 ♂ and 1 ♀. N.W.T.: Cameron Bay, Great Bear Lake, 7.VII.1937 (T. N. Freeman), 4 ♂♂ (2); Bathurst Inlet, 20.VII.1951 (W. I. Campbell), 1 ♂ (1). Yukon: Swim Lake 3200', 16.VI.1949 (E. W. Rockburne), 1 ♀; Rampart House, 9.VII.1951 (J. E. H. Martin), 2 ♀♀; Dawson 3200', 9.VII.1949 (P. F. Bruggeman), 1 ♂ (1). USA: Alaska: Anchorage, 26.VI.1951 (R. S. Bigelow), 1 ♂. Colorado: Doolittle Range 9800', Mt. Evans, 30.VII-2.VIII.1961 (E. W. Rockburne), 2 ♂♂ (1).

FINLAND: Kilpisjärvi, 8.VII.1936 (Lankiala), 1 ♂ (1); Malla subalp., 2.VII.1936 (Lankiala), 1 ♀; Enontekio Karesuanto, 20.VI.1948 (O. Peltonen), 1 ♂ (1); Suecia to Jukkasjärvi, UTM 34W DA8930, 21.VI.1978 (Ingvar Svensson), 2 ♂♂, BMNH; Ytatuostari, 12.III.1935 and VI.1937 (W. Hackman), 1 ♂ and 1 ♀, BMNH. All specimens in the Canadian National Collection of insects, Ottawa, except as indicated otherwise (BMNH = The British Museum of Natural History, now known as The Natural History Museum, London, England).

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ANETIA JAEGERI, DANAUS CLEOPHILE AND
LYCOREA CLEOBAEA FROM JAMAICA
(NYMPHALIDAE: DANAINAE)

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ABSTRACT. Two species of danaid butterflies, *Anetia jaegeri* Ménétriés and *Lycorea cleobaea* Godart, are documented from Jamaica, West Indies, for the first time. The status of a third, *Danaus cleophile* Godart, is reviewed. The biogeographic implications of these species' occurrence on Jamaica are discussed in the context of Caribbean biogeography.

Additional key words: Hispaniola, Cuba, biogeography, vicariance, distribution.

This paper comments on three rare milkweed butterflies (Danainae) from Jamaica, including the first formal records of the genera *Anetia* and *Lycorea* from the island, and speculates on the presence of a second, possibly new species of *Anetia*. Biogeographic implications of the new discoveries are briefly discussed.

Anetia jaegeri Ménétriés

The genus *Anetia* Hübner, once considered to be the most primitive of milkweed butterflies (Forbes 1939), comprises five montane or sub-montane species distributed in three areas: Central America (*A. thirza* Geyer), Cuba (*A. cubana* Salvin, *A. briarea* Godart, *A. pantheratus* Martyn), and Hispaniola (*A. jaegeri*, *A. briarea*, *A. pantheratus*). For many years there has been speculation that *Anetia* also occurs on Jamaica. Based on sightings made by several naturalists, Brown and Heineman (1972) concluded that "it seems possible that there is a species . . . on Jamaica that awaits capture and will probably be found to represent another member in the *cubana-jaegeri* complex."

The Natural History Museum (BMNH, London) recently has received a male *Anetia jaegeri* labelled 'Jamaica, Christiana, Aug. 21 1960.' Christiana lies almost exactly at the center of the island, in the south-western part of the Dry Harbour Mountains, at over 1200 m altitude. The terrain is characterized by pine plantations on the higher hilltops, cultivated ridges, and dense scrub in intervening ravines. This new specimen differs from males of nominate *A. jaegeri*, formerly known only from Hispaniola, by having slightly more extensive yellow mark-



FIG. 1. *Anetia jaegeri*, male, from Christiana, Jamaica, 21.viii. 1960; forewing length 41 mm.; dissection 1773A. Dorsal surface on left, ventral on right.

ings. The wing pattern (Fig. 1) of this individual is thus more similar to that of Hispaniola females rather than males. The genitalia are the same as Hispaniolan *jaegeri*.

A second male specimen, with exactly the same data written in the same hand, is held in the University of Florida collection, Gainesville, Florida. In this case the upperside is almost identical to Hispaniolan males, notably in the size of the yellow spots. On the underside hind-wing, the brown markings are reduced or absent, with only the vertical bar, which extends from the anterior wing margin to the end of the discal cell, remaining prominent. Compared to Hispaniola males in the BMNH collection, this appears to represent one extreme of the normal variation in wing-marking intensity. The relatively fresh wing condition of both specimens, and the collection of more than one specimen on the same day, suggest that *A. jaegeri* is a resident species in central Jamaica.

Danaus cleophile Godart

Danaus (Danaus) cleophile is a second danaine butterfly thought to occur only on Hispaniola and Jamaica. A relatively little-known insect, it is the sister-species of the monarch butterflies (*Danaus (Danaus) plexippus* L. and *D. (D.) erippus* Cramer), and may thus prove to be of great significance in relation to many current speculations about the monarch (see Malcolm & Zalucki 1992).

Danaus cleophile was last collected in Jamaica by Avinoff and Schoumatoff on Mount Diablo, in 1941, in ravines where waterfalls occurred.

As waterfalls are not found on the most well-known part of Mount Diablo, between Evarton and Moneague, the precise locality needs to be re-discovered. Repeated searches in the Hollymount area of Mount Diablo, as recently as June 1992, have been unsuccessful.

Lycorea cleobaea Godart

The second danaine formally recorded from Jamaica for the first time is *Lycorea cleobaea cleobaea*. This is the same subspecies as found on Hispaniola and Puerto Rico, and distinct from *L. c. demeter* Felder and Felder from Cuba (with occasional strays in southern Florida), and the various subspecies of Central and South America. It was first found on Jamaica as larvae feeding on *Carica papaya* L. (Caricaceae), in southwest Kingston, by A. Garel. A single female, which emerged on 2 February 1974, is held in the Institute of Jamaica collection, Kingston. Adults have been seen in xeric regions of southwest Kingston as recently as October 1990, by D. Hopwood. This insect also occurs in xeric habitats in Haiti (Schwartz 1983).

Biogeography

According to Ackery and Vane-Wright (1984), *A. jaegeri* is the sister species of *A. cubana*, and these two together form the sister group to *A. thirza*. The discovery of *A. jaegeri* on Jamaica might thus suggest, on a vicariance hypothesis, that Jamaica and Hispaniola have a more recent history of connection to each other than either has to Cuba. However, Ackery and Vane-Wright (1984) also regarded *A. jaegeri* as a "paraspecies" (cf. "metaspecies" of de Queiroz & Donoghue 1988) because *A. jaegeri* lacks a diagnostic autapomorphy in relation to *A. cubana* and *A. thirza*. On this evidence, the two populations of *A. jaegeri* must be treated as a paraphyletic group, with the implication that one or the other (rather than both together) could form the true sister group of *A. cubana*. Thus, any idea of a special relationship between Hispaniola and Jamaica could not be directly supported by the evidence of *A. jaegeri*.

As *D. cleophile*, also restricted to Hispaniola and Jamaica, is regarded as a cladistically definable species (Ackery & Vane-Wright 1984), this might give credence to a special relationship between the two islands (cf. Miller & Miller 1989) and raise the expectation of eventually finding uniquely defining characteristics for *A. jaegeri* itself. We have no information on the possible monophyly of the Hispaniolan and Jamaican populations of *Lycorea cleobaea cleobaea*. The nominate subspecies extends to Puerto Rico but, as indicated above, the Cuban population of *L. cleobaea* is phenotypically distinct.

Liebherr (1988) has investigated the biogeography of West Indian

carabid beetles of the genus *Platynus*, demonstrating strong links between Hispaniola, Cuba, Jamaica, and Central America. Over the last 50 million years Cuba and Hispaniola may have undergone a complex sequence of fusions and separations, but Jamaica appears to have been separate (but sometimes closer to Hispaniola than now) throughout this period (Liebherr 1988, also see Miller & Miller 1989). Such a scenario provides a ready explanation for *Anetia jaegeri* as a paraspecies, but does not help us to understand the distribution of *Danaus cleophile*. Has *D. cleophile* never occurred on Cuba, has it gone extinct there, or has it simply been overlooked? The new Jamaican records of *Anetia* and *Lycorea* reported here, and the failure to find *D. cleophile* on Jamaica for over 50 years, make the last two possibilities more likely.

As an alternative to a vicariance hypothesis, we could consider dispersal. Darlington (1957) suggested that frogs of the genus *Hyla* entered the Greater Antilles from the Honduras region, reaching Jamaica first, then Hispaniola, and finally Cuba. Such a dispersal route would provide an explanation for both the limited distribution of *Danaus cleophile* and the paraphyly of *A. jaegeri* in relation to *A. cubana*—but there is no compelling reason to single out this particular route in preference to others.

Yet Another Jamaican Danaine?

Before such questions or speculations are pursued on existing evidence, more direct exploration is required. With the addition of *Anetia jaegeri* and *Lycorea cleobaea* to the Jamaican list, the number of milkweed butterflies positively recorded from the island has risen to six (the others being *Danaus cleophile*, *D. eresimus* Cramer, *D. gilippus* Cramer and *D. plexippus*). However, since 1948 there have been several accounts of a large, dark, unidentified butterfly in the mountains of eastern Jamaica, which appear to indicate the existence of a seventh danaine. Brown and Heineman (1972) concluded that the butterfly must be an *Anetia*, but a much darker species than *A. jaegeri*, more like the very distinctive *A. cubana*.

For example, Lewis (1949) reported that in June 1948 Coleman Goin of the University of Florida described a "fairly large, dark butterfly, apparently black with a distinct yellow border along the margin of both fore and hind wings" near the summit of Blue Mountain Peak. On 8 July 1948 Lewis sighted a "large, apparently black butterfly, with a wing spread of nearly four inches" and "a yellow border around the outer edges of both pairs of wings," at Cinchona, several miles to the west of Blue Mountain Peak. Bengry (1949) notes that on 22 April 1949 McCord sighted a butterfly above Mavis Bank, south of Cinchona, which was "black with white and yellow borders on all wings."



FIG. 2. Known distribution of *Anetia jaegeri* (solid circles) in central Jamaica, and the locations of sightings of a darker, *Anetia*-like insect in eastern Jamaica (open symbols) (see also text).

On 2 July 1967, Turner saw a large dark brown or sooty black insect, with pale yellow submarginal bands on both wings, crossing the track one mile north of Barretts Gap on the way to Corn Puss Gap, several miles east of the earlier sightings. On 2 August 1968 a similar insect was observed by Turner, two miles south of Corn Puss Gap, flying 15 ft high in a forest clearing, where it was observed for several minutes. The butterfly was dark brown to sooty black, about four inches in wingspan, and with a clearly visible falcate apex to the forewing. Seen from beneath, the submarginal band on the forewing was pale yellow and broader and more continuous than that of *A. cubana*. The submarginal marking of the hindwing was not opaque like that of the forewing, and was difficult to discern from below.

Both flight pattern and wing markings were superficially similar to the endemic *Papilio homerus* Fabricius, but the unidentified insect was smaller and lacked tails. There was no similarity in flight to either *Papilio pelaus* Fabricius or *Battus polydamas* L., both of which were seen in the vicinity. The eastern localities in which these sightings have been made include habitats with elevations from approximately 450–2250 m, in or adjacent to cloud forest. The distributions of *A. jaegeri* and the unidentified *Anetia*-like insect from eastern Jamaica are shown in Fig. 2.

As Cuba and Hispaniola both harbor three species of *Anetia*, is it possible that there could be two, or even more species on Jamaica? If a form of *A. cubana* is confirmed to occur there in addition to *A. jaegeri*, the biogeographical challenge presented by *Anetia* would become even more interesting.

A concerted effort to rediscover *Anetia* in Jamaica would seem well worthwhile. A search is already in progress (including attempts to relocate *Danaus cleophile*) through Turner's *Caribbean Wildlife Surveys*. Recent advances in our knowledge of the biology of the previously obscure *Anetia* butterflies (Schwartz 1989, Ivie et al. 1990, Ackery in prep.) surely will increase the chances of success.

A key step will involve discovery of the early stages and re-confirmation of the hostplant. DeVries (1987) notes *Metastelma* (Asclepiadaceae) as a possible host for *Anetia thirza* in Costa Rica, while Keith Brown (pers. comm.) knows of *Anetia* having been bred on *Cynanchum* (= *Metastelma* = *Vincetoxicum*) in Cuba, Dominican Republic, Costa Rica, and El Salvador. This suggests likely hosts to be *Cynanchum leptocladum* for *A. jaegeri* in central Jamaica, and *C. fawcetti* or *C. harrisii* for eastern *Anetia* species.

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CHECK LIST OF THE OLD WORLD EPIPASCHIINAE AND
THE RELATED NEW WORLD GENERA *MACALLA* AND
EPIPASCHIA (PYRALIDAE)

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ABSTRACT. Two hundred seventy-three Old World species and 14 New World species belonging to *Macalla* Walker and *Epipaschia* Clemens are included. Information about the taxonomic status of *Macalla*, *Locastra*, *Stericta*, and *Coenodomus* is provided. Twenty-one new synonyms and eighteen new combinations are proposed.

Additional key words: *Pococera* complex, *Locastra*, *Stericta*, *Coenodomus*, *Lista*.

The Epipaschiinae are a large subfamily of over 700 species worldwide. Within the subfamily a monophyletic group of New World genera and species, the *Pococera* complex (Solis 1989) can be recognized. A check list of the *Pococera* complex will be published in the future in the context of a systematic revision and phylogenetic analysis (Solis in press). The remaining taxa are listed herein, including all Old World epipaschiines and New World *Macalla* Walker and *Epipaschia* Clemens. *Macalla* and *Epipaschia* are included because morphological studies (Howard & Solis 1989, Solis 1989) show them to be more closely related to Old World genera than to the New World *Pococera* complex. Some species previously placed in *Macalla* in the Old World are not related to New World *Macalla*. In the present check list these are placed in *Salma* Walker, the next available name (Shaffer et al. in press). Anyone using this list also should refer to the *Checklist of the Lepidoptera of Australia* (Shaffer et al. in press) for further new combinations and synonymies in reference to the Australian fauna. Nevertheless, this list will provide a foundation for anyone wishing to conduct taxonomic work on the Epipaschiinae since the monophyly of the genera is still in question, and the placement of some genera within the Epipaschiinae requires verification.

Some species in the Western Hemisphere were incorrectly associated with *Locastra* Walker and *Stericta* Lederer. The Western Hemisphere species placed in them belong to genera in the *Pococera* complex. Dissection of the types of *L. crassipennis* Walker (synonym of *L. mai-manalis* Walker) and *S. divitalis* (Guenée), the type species of *Locastra* and *Stericta* reveals these genera to be restricted to the Old World.

Coenodomus Walsingham, an Old World genus, is attributed to the North American fauna (Hodges et al. 1983). Two genera, *Dyaria* Neumoegen and *Alippa* Aurivillius, are junior synonyms of *Coenodomus*. In 1893 Neumoegen described *Dyaria* in the Lymantriidae and named

it after his "faithful co-labourer and friend Mr. H. G. Dyar" based on a male specimen supposedly caught in Bangor, Maine. In 1900 Dyar referred *Dyaria* to the Epipaschiinae and synonymized with it *Alippa* Aurivillius, a genus placed previously in the Limacodidae. He stated: "Its occurrence in North America needs verification, in spite of the positive statement published." I have not seen any other specimens in any museum of this genus with collection data referring to the Western Hemisphere. Walsingham described this genus based on material he received from India reared from *Eugenia jambolana* Lamarck (Myrtaceae). *Lista* Walker is revised based on Michael Shaffer's unpublished work at the The Natural History Museum, London, England.

The generic names were crosschecked with *The Generic names of Moths of the World* (Fletcher & Nye 1984). The generic name is followed by the year and page of the citation and the type species in parentheses. Synonyms are listed under the generic or species name. Citations and type localities of all species names, including synonyms, are listed. If the original type locality did not include the modern country, it is provided, followed by the more specific type locality. When no specific locality is given and/or the original general locality is ambiguous, the original general locality is listed.

CHECK LIST

- Agastophanes** Turner, 1937:71. (*zophoxys*-*ta* Turner)
zophoxys Turner, 1937:72. Australia: Queensland: Cape York.
- Anexophana** Viette, 1960a:154. (*robinsonalis* Viette)
robinsonalis Viette, 1960a:155. Madagascar Est: Sahafanjana.
- Araeopaschia** Hampson, 1906:134. (*rufescentalis* Hampson) (not Hampson, 1916a)
demotis (Meyrick, 1887:188) (*Stericta*). West Australia: Geraldton.
normalis (Hampson, 1906:135) (*Spectrotrota*). Australia: Sherlock R.
rufescentalis Hampson, 1906:134. Australia: Geraldton.
- Astrapometis** Meyrick, 1884a:67. (*saburalis* Walker)
saburalis (Walker, 1859:914) (*Pyralis*?). Australia: Moreton Bay.
- Austropaschia** Hampson, 1916a:155. (*porrigens* Hampson)
porrigens Hampson, 1916a:155. W. Australia: Yallingup.
- Axiocrita** Turner, 1913:136. (*cataphanes* Turner)
cataphanes Turner, 1913:136. Australia: Queensland: Kuranda.
- Catalaodes** Viette, 1953:131. (*malgassicalis* Viette)
malgassicalis Viette, 1953:132. Madagascar Est: Fianarantsoa.
- Catamola** Meyrick, 1884a:63. (*funerea* Walker)
Elaphernis Meyrick, 1936:1. (*funerea* Walker)
funerea (Walker, 1863:31) (*Acrobasis*). Australia: Sydney.
- xanthomelalis* (Walker, 1863:32) (*Acrobasis*?). Australia: Sydney.
- Coenodomus** Walsingham, 1888:49. (*hockingi* Walsingham)
Dyaria Neumoegen, 1893:213. (*singularis* Neumoegen)

- Alippa Aurivillus*, 1894:176. (*anomala Aurivillus*)
aglossalis (Warren, 1896:456) (*Scopocera*). India: Khasias. **New combination**
cornucalis (Kenrick, 1907:73) (*Stericta*). Papua New Guinea: Dinawa. **New combination**
dudgeoni Hampson, 1896a:118. Bhután.
fumosalis Hampson, 1903:35. India: Khásis.
hampsoni West, 1931:209. Philippine Islands: Luzon, Benguet, Palili.
hockingi Walsingham, 1888:50. India: Punjab, Kangra Valley.
singularis (Neumoegen, 1893:215) (*Dyaria*). USA: Maine, Bangor.
anomala (Aurivillus, 1894:176) (*Alippa*). Java.
melanochlora (Hampson, 1916a:147) (*Stericta*). Singapore. **New combination**
rotundinidus Hampson, 1891:127. India: Nilgiri.
rubescens (Hampson, 1903:36) (*Stericta*). Sikkim. **New combination**
schausi (West, 1931:210) (*Stericta*). Philippine Islands: Luzon, Benguet, Klondyke. **New combination**
trichasema (Hampson, 1916a:147) (*Stericta*). Sri Lanka: Kitulgala. **New combination**
trissosticha (Turner, 1932:192) (*Orthaga*). Australia: Adelaide R.
Doddiana Turner, 1902:187. (*callizona* Lower)
analamalis Viette, 1960b:207. Madagascar Est: Perinet, Analamazaotra.
callizona (Lower, 1896:155) (*Stericta*). Australia: Queensland: Mackay.
cyanifusalis Marion, 1955:115. Madagascar Est: route d'Anosibé.
Elisabethinia Ghesquière, 1942:236. (*cosmia* Ghesquière)
cosmia Ghesquière, 1942:237. Zaire: Elisabethville.
Ephedrophila Dumont, 1928:28. (*lucasi* Mabille)
algerialis (Hampson, 1900:377) (*Ulotricha*). Algiers: Biskra.
jordanalis (Rebel, 1902:100) (*Lepidogma*). Jordan.
constantialis (Hampson, 1906:123) (*Anartula*). Egypt: Suez Canal.
lucasi (Mabille, 1907:308) (*Ulotricha*). Tunisia.
- Epilepia** Janse, 1931:466. (*melanosparsalis* Janse)
dentatum (Matsumura and Shibuya, 1927 in Shibuya, 1927a:349) (*Macalla*). Formosa: Kyoto. Lectotype designated (Inoue and Yamanaka, 1975); Kyoto, Suzuki.
melanobrunnea (Janse, 1922:21) (*Macalla*). South Africa: Hope Fountain.
melanosparsalis (Janse, 1922:24) (*Macalla*). South Africa: Hope Fountain.
confusa (Janse, 1922:26) (*Macalla*). South Africa: Bulawayo.
simulata Janse, 1931:466. N. Nigeria: Agbaja.
Epipaschia Clemens, 1860:14. (*superatalis* Clemens)
mesoleucalis (Hampson, 1916b:129) (*Pococera*). Fr. Guiana: St. Laurent Maroni.
furseyalis (Schaus, 1922:233) (*Macalla*). Guatemala: Quirigua. **New synonym**
ochrotalis (Hampson, 1906:139) (*Macalla*). Fr. Guiana: Cayenne.
superatalis Clemens, 1860:14. USA: Connecticut, Farmington.
Eublemmodes Gaede, 1917:389. (*contumacialis* Gaede)
contumacialis Gaede, 1917:389. Cameroon.
- Heminomistis** Meyrick, 1933:436. (*melanthes* Meyrick)
melanthes Meyrick, 1933:436. Thailand.
Lacalma Janse, 1931:464. (*porphyrealis* Kenrick)
albirufalis (Hampson, 1916a:137) (*Macalla*). New Guinea: Snow Mts., Oetakwa R.
argenteorubra (Hampson, 1916a:138) (*Macalla*). New Guinea: Mt. Golaith.
papuensis (Warren, 1891:431) (*Stericta*). New Guinea.
porphyrealis (Kenrick, 1907:71) (*Macalla*). Papua New Guinea: Ekeikei, Kebea, Dinawa.
Lameera Ghesquière, 1942:238. (*ensipalpus* Ghesquière)
ensipalpis Ghesquière, 1942:239. Zaire: Lulua, Kapanga.
Lamida Walker, [1859] 1858:252. (*moncusalis* Walker)
Allata Walker, 1863:110. (*penicillata* Walker)
buruensis Janse, 1931:461. Indonesia: Buru.

- mediobarbalis* (Hampson, 1916a:135) (*Macalla*). Sikhim.
- moncusalis* Walker, [1859] 1858:252. Hindostan.
- penicillata* (Walker, 1863:111) (*Allata*). Hindostan.
- obscura* (Moore, 1888:201) (*Orthaga*). India: Darjiling.
- sordidalis* (Hampson, 1916a:136) (*Macalla*). Sikhim.
- proximalis* (Caradja, 1925:53) (*Macalla*). China: Canton.
- Lepidogma** Meyrick, 1890:472. (*tamaricalis* Mann)
- Precopia* Ragonot, 1891:18 (key), 67. (*atomalis* Christoph)
- Asopina* Christoph, 1893:36. (*obratialis* Christoph)
- ambifaria* Hering, 1901:22. Sumatra.
- melanopalis* Hampson, 1906:130. Borneo: Sandakan.
- atomalis* (Christoph, 1887:166) (*Hypotia*). Turkey: Tekké.
- chlorophilalis* Hampson, 1912:1257. Sri Lanka: Maskeliya.
- chrysochloralis* Hampson, 1916a:130. New Guinea: Fak-fak.
- dentilinealis* Hampson, 1906:130. Kenya: Maungu-Inkuhwa.
- farinodes* de Joannis, 1929:627. Vietnam: Tonkin.
- flagellalis* Hampson, 1906:129. Borneo: Kuching.
- hyrcanalis* Amsel, 1961:392. Iran.
- latifasciata* (Wileman, 1911:230) (*Eulocastra*). Japan: Hondo, Yoshino.
- megaloceros* Meyrick, 1934:531. Zaire: Elisabethville.
- melaleucalis* Hampson, 1906:129. Ghana: Ashanti: Kumassi.
- melanobasis* Hampson, 1906:129. Japan: Yokohama.
- tripartita* (Wileman-South, 1917a:128) (*Stericta*). Taiwan: Kanshirei.
- melanolopha* Hampson, 1912:1258. Sri Lanka: Kegalle.
- dubia* (Wileman-South, 1917a:128) (*Stericta*). Taiwan: Kanshirei.
- melanospila* Hampson, 1916a:129. Ghana: Bibianaha.
- minimalis* Hampson, 1916a:129. Sri Lanka: Perdeniya.
- obatratis* (Christoph, 1877:264) (*Asopina*). Turkmeniya (USSR): Krasnovodsk.
- olivalis* (Swinhoe, 1895:301) (*Hypsopygia*). India: Mahableshwar.
- novalis* (Warren, 1896:463) (*Ulotrichodes*). India: Bombay.
- rubricalis* Hampson, 1906:131. Zimbabwe: Salisbury.
- rufescens* Hampson, 1896a:112. Bhutan.
- tamaricalis* (Mann, 1873:124) (*Hypotia*). Italy: Tuscany.
- vafera* (Swinhoe, 1884:523) (*Hypotia*). Pakistan: Kurrachee.
- wiltshirei* Amsel, 1949:299. Iraq: Bagdad.
- Leptoses** Chesquière, 1942:236. (*sophronicos* Chesquière)
- sophronicos* Chesquière, 1942:236. Zaire: Elisabethville.
- Lista** Walker, 1859:877. (*genisusalis* Walker) **Revised status**
- Paracme* Lederer, 1863:338. (*insulsalis* Lederer) **New synonym**
- Craneophora* Christoph, 1881:1. (*ficki* Christoph) **New synonym**
- Belonepholis* Butler, 1889:89. (*striata* Butler) **New synonym**
- carniola* (Hampson, 1916a:146) (*Stericta*). Papua New Guinea: Dinawa.
- New combination**
- ficki* (Christoph, 1881:1) (*Craneophora*). Amur. **New combination**
- striata* (Butler, 1889:90) (*Belenopholis*). India: Dharmasala. **New synonym, new combination**
- haraldusalis* (Walker, [1859] 1858:160) (*Locastra?*). Borneo: Sarawak. **New combination**
- genisusalis* Walker, 1859:877. Borneo: Sarawak. **New synonym**
- insulsalis* (Lederer, 1863:339) (*Paracme*). China: Ningpo. **New combination**
- rubiginetincta* (Caradja, 1925:314) (*Stericta*). China: Canton. **New synonym, new combination**
- plinthochroa* (West, 1931:211) (*Stericta*). Philippine Islands: Luzon, Benguet, Palii. **New combination**
- sumatrana* (Hering, 1901:25) (*Craneophora*). Sumatra. **New combination**
- variegata* (Moore, 1888:203) (*Scopocera*). India: Darjiling. **New combination**
- Locastra** Walker, [1859] 1858:158. (*maimonalis* Walker). By subsequent designation.
- Taurica* Walker, [1866] 1865:1268. (*muscosalis* Walker)
- ardua* Swinhoe, 1902:181. Fiji.

- drucei* Bethune-Baker, 1905:94. Fiji: Nausori.
- bryalis* de Joannis, 1929:631. Vietnam: Tonkin.
- maimonalis* (Walker, [1859] 1859:159) (*Locastra*). Borneo: Sarawak.
- crassipennis* (Walker, 1857:558) (*Eurois*?). Bangladesh: Silhet.
- muscosalis* Walker, [1866] 1865:1269) (*Taurica*). North China.
- sikkima* (Moore, 1888:202) (*Taurica*). India: Darjiling.
- cristalis* (Hampson, 1893:157) (*Locastra*). Sri Lanka.
- pachylepidalis* Hampson, 1896a:119. Bhután.
- Macalla** Walker, [1859] 1858:155. (*thyrsalis* Walker)
- Aradrapha* Walker, [1866] 1865:1257. (*mixtalis* Walker)
- Mochlocera* Grote, 1876:157. (*zelleri* Grote)
- Pseudomacalla* Dognin, 1908:26. (*noctuiipalpis* Dognin)
- arctata* (Druce, 1902:325) (*Cecidiptera*, missp.). Peru: Chanchamayo.
- finstanalis* Schaus, 1922:232. Guatemala: Quirigua.
- vulstana* Schaus, 1922:234. Peru: Yahuar mayo. **New synonym**
- hyalinalis* Amsel, 1956:55. Venezuela: Maracay.
- nebulosa* Schaus, 1912:667. Costa Rica: Avangarez.
- niveorufa* Hampson, 1906:139. Panama: Cana Mines.
- noctuiipalpis* (Dognin, 1908:26) (*Pseudomacalla*). Argentina: Tucuman.
- sinualis* Jones, 1912:443. Brazil: Paraná: Castro. **New synonym**
- symmetrica* Amsel, 1956:56. Venezuela: Maracay. **New synonym**
- asymmetrica* Amsel, 1956:56. Venezuela: Maracay. **New synonym**
- pallidomedia* Dyar, 1910:136. Guyana: Hoorie.
- macallalis* (Schaus, 1934:111) (*Chloropaschia*). Brazil: Rio de Janeiro: Campo Bello. **New synonym**
- phaeobasalis* Hampson, 1916a:144. Cuba: Santiago.
- regalis* Jones, 1912:443. Brazil: Paraná: Castro.
- euryleuca* Hampson, 1916a:140. Peru: San Gaban. **New synonym**
- hyutanahana* Schaus, 1925:27. Brazil: Hyutanahan, Rio Purús. **New synonym**
- thyrsalis* Walker, [1859] 1858:156. Honduras.
- mixtalis* (Walker, [1866] 1865:1257) (*Aradrapha*). Honduras.
- zelleri* (Grote, 1876:157) (*Mochlocera*). USA: Texas. **New combination**
- Mimaglossa** Warren, 1891:427. (*habitalis* Guenée)
- crypserythra* (Turner, 1904:198) (*Epipaschia*). Australia: Tasmania: Hobart.
- habitalis* (Guenée, 1854:125) (*Glossina*). Australia.
- cervinalis* (Walker, 1862:121) (*Pyralis*). Australia: Tasmania.
- revulsa* Warren, 1891:428. Australia.
- nauphalis* (Walker, 1859:272) (*Pyralis*?). Country unknown.
- porphyralis* (Walker, [1866] 1865:1213) (*Pyralis*). Australia: Swan River.
- subcostella* (Walker, 1869:81) (*Acrobasis*). Australia.
- Neopaschia** Janse, 1922:20. (*flavociliata* Janse)
- flavociliata* Janse, 1922:20. South Africa: Barberton.
- lematrei* Viette, 1965:217. Malagasy Republic: Andapa.
- nigromarginata* Viette, 1953:130. Madagascar: Saigon.
- Noctuides** Staudinger, 1892:466. (*melanophia* Staudinger)
- Anartula* Staudinger, 1893:78. (*melanophia* Staudinger)
- Arnatula* Hampson, 1896b:454. (subs. missp.)
- Parorthaga* Hampson, 1896a:110. (*euryptera* Meyrick)
- albifascia* (de Joannis, 1929:626) (*Anartula*). Vietnam: Tonkin.
- griseoviridis* (Pagenstecher, 1907:130) (*Anartula*). Madagascar.
- melanochyta* (Meyrick, 1933:435) (*Anartula*). Zaire: Katakumba.
- melanophia* (Staudinger, 1892:466) (*Anartula*). USSR: Amur Region.
- euryptera* (Meyrick, 1894:476) (*Balanotis*). Malay Archipelago: Sambawa.
- thurivora* (Meyrick, 1932:319) (*Anartula*). Sri Lanka: Galle.
- tympnanophora* (Turner, 1904:193) (*Anartula*). Australia: Queensland: Eumundi.

- Nyctereutica** Turner, 1904:192. (*asbolopsis* Turner).
- Diastrophica* Turner, 1937:72. (*tephrophanes* Turner)
- asbolopsis* Turner, 1904:192. Australia: Queensland: Townsville.
- capnopis* (Meyrick, 1885:439) (*Catamola*). Australia: New South Wales: Mt. Kosciusko.
- elassota* (Meyrick, 1884b:280) (*Catamola*). South Australia: Quorn.
- melanophorella* (Walker, 1866:1831) (*Gelechia*). Australia: Sydney.
- tephrophanes* (Turner, 1937:72) (*Dias-trophica*). Australia: Queensland.
- tornotis* (Meyrick, 1887:188) (*Stericta*). Australia: Queensland: Helidon.
- Obutobea** Ghesquière, 1942:239. (*chrysophora* Ghesquière)
- chrysophora* Ghesquière, 1942:240. Zaire: Eala.
- Odontopaschia** Hampson, 1903:34. (*vires-cens* Hampson).
- economia* Turner, 1913:133. Australia: Queensland: Kuranda.
- stephanuchra* Tams, 1935:255. Samoa.
- virescens* Hampson, 1903:34. India: Khâsis.
- Omphalepia** Hampson, 1906:190. (*sobria* Hampson)
- dujardini* Viette, 1967:56. Madagascar Ouest: Andranomena.
- sobria* Hampson, 1906:191. British East Africa.
- Omphalota** Hampson, 1899:479. (*chlorobasis* Hampson)
- chlorobasis* Hampson, 1899:480. India: Simla.
- Oncobela** Turner, 1937:72. (*philobrya* Turner)
- philobrya* Turner, 1937:73. Australia: Queensland: Cape York.
- Orthaga** Walker, [1859] 1858:191. (*euad-rusalis* Walker)
- Edeta* Walker, [1859] 1858:198. (*ica-rusalis* Walker)
- Pannucha* Moore, 1888:199. (*aenes-cens* Moore)
- Probosciphora* Warren, 1891:429. (*tritonalis* Walker)
- Hyperbalanotis* Warren, 1891:433. (*achatina* Butler)
- achatina* (Butler, 1878:1856) (*Glossina*). Japan: Yokohama.
- aenescens* (Moore, 1888:200) (*Pannucha*). India: Darjiling.
- vicinalis* (Snellen, 1890:567) (*Pannucha*). India: Darjiling.
- amphimelas* Turner, 1913:140. Australia: N. Territory: Port Darwin.
- asbolaea* (Meyrick, 1938:73) (*Catamola*). West Java: Mt. Guntur: Garoet.
- auroviridalis* Hampson, 1896a:126. Sikh-im: Bhután.
- basalis* (Moore, 1888:200) (*Pannucha*). India: Darjiling.
- bipartalis* Hampson, 1906:147. Singapore.
- castanealis* (Kenrick, 1907:72) (*Locastra*). Papua New Guinea: Dinawa.
- chionalis* Hampson, 1906:147. Singapore.
- chionalis* Kenrick, 1907:73. Papua New Guinea: Ekeikei, Babouni, Kebea, Dinawa.
- columbalis* Kenrick, 1907:74. Papua New Guinea: Kebea.
- confusa* Wileman-South, 1917a:128. Taiwan: Kanshirei.
- cryptochalcis* de Joannis, 1927:234. Mozambique: Lourenço-Marquês: Makulane.
- disparoidalis* Caradja, 1925:59. China: Shanghai.
- durranti* West, 1931:211. Philippines Islands: Luzon, Benguet, Pauai, Haight's Place.
- ecphoeana* Hampson, 1916a:152. Br. N. Guinea: Mt. Kebea.
- edetalis* Strand, 1919:52. Taiwan: Kosempo.
- erebochlaena* Meyrick, 1938:75. South Central Java: Djokjakarta.
- euadrusalis* Walker, [1859] 1858:191. Borneo: Sarawak.
- acontialis* Walker, 1863:103. Borneo: Sawawak.
- eumictalis* Hampson, 1916a:150. New Guinea: Fak-fak.
- euryzona* Hampson, 1896a:128. Burma: E. Pegu.
- exvinacea* (Hampson, 1891:127) (*Balanotis*). India: Nilgiri.
- ferrealis* Hampson, 1906:145. Australia: Queensland, Townsville.
- fuliginosa* (Rothschild, 1915:116) (*Polyphota*). New Guinea: Utakwa River.
- fumida* (Hering, 1901:32) (*Pannucha*). Sumatra.
- fuscofascialis* Kenrick, 1907:74. Papua New Guinea: Dinawa and Kebea.
- haemorphoralis* Hampson, 1916a:150. New Guinea: Setakwa R.

- hemileuca* Hampson, 1916a:149. New Guinea: Fak-fak.
- icarusalis* (Walker, [1859] 1858:199) (*Edeta*). Borneo: Sarawak.
- irrorata* (Hampson, 1893:156) (*Balano-tis*). Sri Lanka.
- leucatma* (Meyrick, 1932:321) (*Balano-tis*). Sri Lanka: Peradeniya.
- leucolophota* Hampson, 1916a:151. New Guinea: Snow Mts: Oetakwa R.
- lithochroa* Hampson, 1916a:152. N. Australia: Port Darwin.
- mangiferae* Misra, 1932:539. India.
- melanoperalis* Hampson, 1906:146. Borneo: Pulo Laut.
- meyricki* West, 1931:211. Philippine Islands: Luzon, Benuet, Palali.
- mixtalis* Walker, 1863:104. Borneo: Sarawak.
- molleri* Hampson, 1896a:126. Sikhim.
- olivacea* (Warren, 1891:433) (*Hyperba-lanotis*). Japan.
- amurensis* (Hampson, 1900:376) (*Macalla*). Amurland: Ussuri.
- shisalis* (Strand, 1919:53) (*Stericta*). Taiwan: Shisa.
- onerata* (Butler, 1879b:447) (*Bleptina*). Japan.
- grisealis* Wileman, 1911:366. Japan: Yokohama.
- phaeopteralis* Lower, 1902:664. Australia: Queensland: Duaringa.
- picta* (Warren, 1895:461) (*Stericta*). Australia: Queensland.
- percnodes* Turner, 1905:63. Australia: Queensland: Kuranda.
- polyscia* (Turner, 1913:138) (*Epipaschia*). Australia: Queensland: Cairns.
- prionosticha* Turner, 1925a:45. Australia: Queensland: Coolangatta.
- rhodoptila* (Meyrick, 1932:320) (*Balano-tis*). Sri Lanka: Galle.
- roseiplaga* Hampson, 1896a:124. India: Bombay.
- rubridiscalis* Hampson, 1906:146. Australia: Queensland.
- rudis* (Walker, 1862:115) (*Locastra*). Hindostan.
- semialba* Meyrick, 1932:319. Malaya: Kuala Lumpur.
- semieburnea* Roepke, 1932:99. Celebes: Tonselama.
- seminivea* (Warren, 1895:463) (*Stericta*?). Australia: Queensland.
- chionopa* (Lower, 1896:155) (*Stericta*). Australia: Queensland: Brisbane.
- subbasalis* (Hering, 1901:30) (*Pannucha*). Sumatra.
- thyrisalis* (Walker, 1858:167) (*Bertula*). Australia: Sydney.
- nigricalis* (Walker, 1862:120) (*Pyralis*). Australia: Tasmania.
- tritonialis* (Walker, 1859:906) (*Pyralis*). Borneo: Sarawak.
- rotundalis* Walker, 1863:106. Borneo: Sarawak.
- umbrimargo* de Joannis, 1927:235. Mozambique: Lourenço-Marquês: Makulane.
- vitialis* (Walker, 1859:897) (*Pyralis*). Sri Lanka.
- helvialis* (Walker, 1859:915) (*Pyralis*). Country unknown.
- altusalis* (Walker, 1859:1022) (*Pyralis*). Obj. repl. name.
- Parastericta** Janse, 1931:486. (*lanata* Janse)
- lanata* Janse, 1931:486. Indonesia: Buru.
- Peplochora** Meyrick, 1933:437. (*zalalgae* Meyrick)
- zalalgae* Meyrick, 1933:437. Sri Lanka: Gampola.
- Plumiphora** Janse, 1931:485. (*pratti* Janse)
- pratti* Janse, 1931:485. Sumatra: Barisan Range.
- Plutopaschia** Hampson, 1917:361. (*sinapis* Rothschild)
- sinapis* (Rothschild, 1915:115) (*Stericta*). New Guinea: Utaikwa River.
- Poliopaschia** Hampson, 1916a:156. (*brachypalpia* Hampson)
- brachypalpia* Hampson, 1916a:156. W. Australia: Yallingup.
- Polylophota** Hampson, 1906:189. (*barbarossa* Hampson)
- arruensis* (Kenrick, 1912:547) (*Macalla*). New Guinea: Arfak Mts.
- atriplagalalis* Hampson, 1916a:146. New Guinea: Fak-fak. **New synonym, new combination**
- klossi* Rothschild, 1915:116. New Guinea: Canoe Camp.
- senilis* Janse, 1931:479. New Guinea: Arfak Mts., Angi lakes.
- barbarossa* Hampson, 1906:189. Papua New Guinea: Moroka.
- truncalis* Kenrick, 1907:72. Papua New Guinea: Dinawa. **New synonym, new combination**
- Rhynchopaschia** Hampson, 1906:190. (*melanolopha* Hampson)
- chalcospaera* Meyrick, 1934:532. Zaire: Elisabethville.

- hemichlora* Meyrick, 1934:531. Zaire: Elisabethville.
- melanolopha* Hampson, 1906:190. Zimbabwe.
- reducta* Janse, 1931:482. South Africa: Barberton.
- virescens* Hampson, 1916a:154. Ghana: Bibianaha.
- Salma** Walker, 1863: 107. (*recurvalis* Walker)
- Exacosmia* Walker, 1864:609. (*rubiginosa* Walker)
- Calinipaxa* Walker, 1865:1218. (*validalis* Walker)
- Parasarama* Warren, 1890:474. (*cuproviridalis* Moore)
- Orthotrichophora* Warren, 1891:429. (*syrictusalis* Walker)
- Heterobella* Turner, 1904:193. (*triglochis* Turner)
- Enchesphora* Turner, 1913:141. (*poliophanes* Turner)
- aenochroa* (Hampson, 1906:136) (*Macalla*). Brit. N. Guinea: Moroka.
- albifurcalis* (Hampson, 1916a:144) (*Macalla*). Travancore: Pirmád.
- amauiropsis* (Turner, 1925b:117) (*Epipaschia*). Tasmania.
- amica* (Butler, 1879b:447) (*Locastra*). Japan.
- apicalis* (Kenrick, 1907:71) (*Macalla*). Papua New Guinea: Kebea, Dinawa, Babouni, Ekeikei.
- polypsamma* (Turner, 1937:74) (*Epipaschia*). Australia: North Queensland: Kuranda.
- atricinctalis* (Hampson, 1916a:141) (*Macalla*). India: Travancore: Pirmád.
- atrox* (Caradja, 1926:170) (*Macalla*). Japan.
- aureobasilis* (Caradja, 1932:10) (*Macalla*). China: Amoy, Canton.
- baibarana* (Shibuya, 1928:101) (*Macalla*). Taiwan: Baibara.
- basiochra* (Turner, 1937:75) (*Epipaschia*). Australia: North Queensland: Cape York.
- brachyscopalis* (Hampson, 1912:1258) (*Macalla*). Sri Lanka: Maskeliya.
- camphorella* (de Joannis, 1929:629) (*Macalla*). Vietnam: Tonkin.
- caradriniformis* (Kenrick, 1907:70) (*Macalla*). Papua New Guinea: Dinawa and Ekeikei.
- carbonifera* (Meyrick, 1932:319) (*Lamida*). India: U.P.: Dehra Dun.
- chlorographalis* (Hampson, 1916a:138) (*Macalla*). New Guinea: Fak-fak.
- chlorophoenia* (Turner, 1913:137) (*Macalla*). Australia: Queensland: Mt. Tambourine.
- cholica* (Meyrick, 1884a:66) (*Cacozelia*). Australia: Queensland: Duarina.
- lygropa* (Turner, 1905:62) (*Epipaschia*). Australia: Queensland: Too-woomba.
- cinerascens* (Warren, 1891:431) (*Stericta*). Australia: New South Wales: Parramatta.
- cletolis* (Turner, 1905:61) (*Epipaschia*). Australia: Queensland: Kuranda.
- chloanthes* (Turner, 1913:139) (*Epipaschia*). Australia: Queensland: Kuranda.
- congenitalis* (Caradja, 1931:205) (*Macalla*). China: Kwanhsien.
- conjuncta* (Warren, 1896:454) (*Parasarama*). India: Khasias.
- cupreotincta* (Janse, 1922:25) (*Macalla*). South Africa: Umtali.
- cuproviridalis* (Moore, 1867:87) (*Locastra*). Bengal, Darjiling.
- curturalis* (Kenrick, 1907:70) (*Macalla*). Papua New Guinea: Dinawa.
- derogatella* (Walker, 1863:30) (*Acrobasis*). Borneo: Sarawak.
- diaprepes* (Turner, 1925a:45) (*Macalla*). Australia: N. Queensland: Kuranda.
- dimidialis* (Snellen, 1890:568) (*Pannucha*). India: Darjiling.
- dochmoscia* (Turner, 1905:61) (*Macalla*). Australia: Queensland: Kuranda.
- dubiosalis* (Caradja, 1925:56) (*Macalla*). China: Lienping.
- ebenina* (Turner, 1904:197) (*Macalla*). Australia: Queensland: Brisbane.
- elatalis* (Caradja, 1925:52) (*Macalla*). China: Canton.
- eumictalis* (Hampson, 1912:1259) (*Macalla*). Sri Lanka: Maskeliya.
- eupepla* (Turner, 1915:35) (*Macalla*). Australia: Queensland: Kuranda.
- exrufescens* (Hampson, 1896a:116) (*Macalla*). Sikhim.
- fasciculata* (Hampson, 1906:137) (*Macalla*). Natal.
- fasciolata* (Rothschild, 1915:114) (*Macalla*). New Guinea: Utakwa River.
- flavicollaris* (Hampson, 1916a:135) (*Macalla*). New Guinea: Fak-fak.
- fulvitinctalis* (Hampson, 1906:138) (*Macalla*). Kenya: Taru.
- galeata* (Hampson, 1906:136) (*Macalla*). Australia: Sherlock R.
- glaucochrysalis* (Hampson, 1906:140) (*Macalla*). Borneo: Sandakan.

- glyceropa* (Turner, 1937:73) (*Macalla*).
Australia: Queensland: Brisbane.
- grisealis* (Caradja, 1925:51) (*Macalla*).
China: Canton.
- hicanodes* (Turner, 1937:74) (*Epipaschia*). Australia: Denmark.
- hoenei* (Caradja, 1931:4) (*Macalla*). China: Mokanshan.
- hupehensis* (Hampson, 1916a:145) (*Macalla*). C. China: Hupeh Prov: Lushin-Tze.
- hyponalis* (Hampson, 1899:480) (*Macalla*). Sikkim.
- hypoxantha* (Hampson, 1896b:465) (*Macalla*). Sikkim.
- ignezonalis* (Hampson, 1906:140) (*Macalla*). Sierra Leone.
- impurella* (Caradja, 1925:55) (*Macalla*). China: Shanghai.
- kwangtungialis* (Caradja, 1925:54) (*Macalla*). China: Lienping.
- lakasy* (Viette, 1981:315) (*Macalla*). Madagascar Ouest: Marosely.
- lithochlora* (Lower, 1896:154) (*Epipaschia*). Australia: Queensland: Brisbane.
- lophotalis* (Hampson, 1900:375) (*Macalla*). Armenia: Zeitun: Mardin.
- madegassalis* (Viette, 1960a:154) (*Macalla*). Madagascar Ouest: Sud de Morondara.
- malgassica* (Kenrick, 1917:97) (*Macalla*). Madagascar.
- marmorea* (Warren, 1891:432) (*Stericta*). Australia: Tasmania: Hobart.
- mauritanica* (Amsel, 1953:1446) (*Macalla*). Mauritania: Tagant: Haceira.
- melanobasis* (Hampson, 1906:139) (*Macalla*). Zimbabwe.
- melapastalis* (Hampson, 1906:136) (*Macalla*). Zimbabwe: Salisbury.
- melli* (Caradja and Meyrick, 1934:145) (*Macalla*). China: Kwangtung.
- mesaleucalis* (Hampson, 1916a:136) (*Macalla*). Province Wellesley.
- metachryseis* (Hampson, 1906:141) (*Macalla*). British East Africa: Eb Urru.
- metasarcia* (Hampson, 1903:35) (*Macalla*). Sikkim.
- metaxanthalis* (Hampson, 1916a:142) (*Macalla*). New Guinea: Fak-fak.
- minoralis* (Hampson, 1906:137) (*Macalla*). Singapore.
- miosuari* (Kenrick, 1912:547) (*Macalla*). New Guinea: Mioswar I.
- mnesibrya* (Meyrick, 1884:71) (*Balanot*).
- mis*. Australia: New South Wales: Murrurundi.
- mnariar* (Turner, 1905:60) (*Macalla*). Australia: Queensland: Kuranda.
- elaea* (Hampson, 1906:135) (*Macalla*). New Guinea: Fergusson I.
- mnimomima* (Turner, 1913:137) (*Macalla*). Australia: Queensland: Atherton.
- nankingialis* (Caradja, 1925:54) (*Macalla*). China: Nanking.
- nephelodes* (Turner, 1933:170) (*Epipaschia*). Australia: Queensland: Yepoon.
- nubilalis* (Hampson, 1893:157) (*Stericta*). Sri Lanka.
- nyctichroalis* (Hampson, 1916a:139) (*Macalla*). Br. New Guinea: Sogeri.
- nyctizonalis* (Hampson, 1916a:139) (*Macalla*). Philippines: Manila.
- obliquilineata* (Shibuya, 1928:102) (*Macalla*). Taiwan: Baibara.
- ochroalis* (Hampson, 1916a:142) (*Macalla*). Sri Lanka: Eppawela.
- olivaceoalba* (Rothschild, 1915:115) (*Stericta*). New Guinea: Utaqua River.
- olivalis* (Kenrick, 1912:547) (*Macalla*). New Guinea: Arfak Mts.
- olivaris* (Hampson, 1916a:140) (*Macalla*). Ghana: Bibianaha.
- soudanensis* (Rothschild, 1921:226) (*Pyrallis*). Africa.
- peloscia* (Turner, 1913:138) (*Macalla*). Australia: Queensland: Kuranda.
- pentabela* (Turner, 1915:34) (*Macalla*). Australia: New South Wales: Mt. Kosciusko.
- peratophaea* (Turner, 1937:75) (*Epipaschia*). Australia: Queensland: Cape York.
- perdentalis* (Kenrick, 1907:71) (*Macalla*). Papua New Guinea: Dinawa, Kebea.
- phaeoperalis* (Hampson, 1916a:141) (*Macalla*). Sri Lanka: Galgama.
- phidiasalis* (Walker, [1859] 1858:166) (*Bertula*). Borneo: Sarawak.
- philiasalis* (Walker, 1863:104) (*Orthaga*). Borneo: Sarawak.
- plicatalis* (Hampson, 1903:35) (*Macalla*). Sri Lanka: Matale.
- plumbeopticalis* (Hampson, 1916a:143) (*Macalla*). New Guinea: Fak-fak.
- polychroalis* Kenrick, 1907:73. Papua New Guinea: Dinawa.
- pomalis* (Kenrick, 1907:70) (*Macalla*). Papua New Guinea: Dinawa.
- poliophanes* (Turner, 1913:141) (*En-*

- chesphora*). Australia: N. Territory: Port Darwin.
- pretiosalis* (Caradja, 1925:55) (*Macalla*). China: Shanghai, Kiangsi.
- pseudopinguinalis* (Caradja, 1925:56) (*Macalla*). China: Lienping.
- purpureopicta* (Hampson, 1916b:170) (*Macalla*). Somaliland.
- pyrastis* (Meyrick, 1887:190) (*Stericta*). Australia: New South Wales: Newcastle.
- ferruginea* (Lucas, 1894:156) (*Balanotis*). Australia: Brisbane.
- recurvalis* Walker, 1863:107. Borneo: Sarawak.
- rubiginosa* (Walker, 1865:609) (*Exacosmia*). Australia.
- malanospilellus* (Walker, 1866:1759) (*Crambus*?). Australia: Sydney.
- crypsaula* (Meyrick, 1887:191) (*Balanotis*). Australia: New South Wales: Sydney.
- ridiculalis* (Caradja, 1925:56) (*Macalla*). China: Canton.
- ribripalpalis* (Hampson, 1916a:137) (*Macalla*). New Guinea: Mt. Goliath.
- rugosalis* (Hampson, 1916a:142) (*Macalla*). Australia: Rook I.
- rufibarbalis* (Hampson, 1903:34) (*Macella*, missp.). Sikhim.
- rufitinctalis* (Warren, 1896:455) (*Parasarama*). Borneo: Sarawak.
- sagarisalis* (Walker, [1859] 1858:160) (*Locastra*). Borneo: Sarawak.
- scoporhyncha* (Hampson, 1896a:114) (*Macalla*). Sikhim.
- seyrigalis* (Viette, 1960a:154) (*Macalla*). Archipel des Comores: Mayotte: Convalescence.
- shanghaiella* (Caradja, 1925:53) (*Macalla*). China: Shanghai.
- shibuyai* (West, 1931:208) (*Macalla*). Philippine Islands: Luzon, Benguet, Palali.
- streptomela* (Lower, 1896:156) (*Stericta*). Australia: Queensland: Duaringa.
- syrichtusalis* (Walker, [1859] 1858:165) (*Bertula*). Borneo: Sarawak.
- pyralisalis* (Walker, 1863:105) (*Orthaga*). Borneo: Sarawak.
- tegulalis* (Walker, 1863:105) (*Orthaga*). Borneo: Sarawak.
- tenebrosalis* (Kenrick, 1907:71) (*Macalla*). Papua New Guinea: Kebea, Ekeikei, Babouni.
- tholoeessa* (Turner, 1925b:116) (*Catamola*). Australia: Tasmania.
- triglochis* (Turner, 1904:194) (*Heterobel-la*). Australia: Queensland: Brisbane.
- umbrosalis* (Hampson, 1916a:143) (*Macalla*). Papua New Guinea: Mt. Kebea.
- unipunctalis* (Kenrick, 1907:70) (*Macalla*). Papua New Guinea: Dinawa.
- vadoni* (Viette, 1981:316) (*Macalla*). Madagascar Est: baie d'Antongil.
- validalis* (Walker, 1865:1218) (*Calinipaxa*). Borneo: Sarawak.
- minor* (Moore, 1888:203) (*Scopocera*). India: Darjiling.
- fumosalis* (Warren, 1896:461) (*Peucecla*). India: Khasias.
- costimacula* (Wileman-South, 1917b:175) (*Pyralis*). Formosa: Rantai-zan.
- viridetincta* (Caradja, 1925:52) (*Macalla*). China: Lienping, Amoy, Canton, Kuling.
- viridirufalis* (Hampson, 1916a:145) (*Macalla*). New Guinea: Fak-fak.
- wollastoni* (Rothschild, 1915:114) (*Macalla*). New Guinea: Uakwa River.
- zophera* (Turner, 1904:196) (*Macalla*). Australia: Queensland: Burpengary.
- mixtirosalis* (Hampson, 1906:135) (*Macalla*). Australia: Queensland: Dawson District.
- Shoutedenidea** Ghesquière, 1942:235. (*ophigona* Ghesquière)
- ophigona* Ghesquière, 1942:235. Zaire: Kai Bumba.
- Sparactica** Meyrick, 1938:74. (*eustola* Meyrick)
- eustola* Meyrick, 1938:75. West Java: Mt. Guntur: Garoet.
- Spectrotrota** Warren, 1891:426. (*fimbrialis* Warren)
- erythrolepiea* Hampson, 1916a:134. Formosa: Arizan.
- catena* Wileman-South, 1917a:127. Taiwan: Arizan.
- fimbrialis* Warren, 1891:427. Australia.
- Speiroceras** Chrétien, 1911:12. (*pectinellum* Chrétien)
- pectinellum* Chrétien, 1911:12. Mauritania: Biskra.
- Stericta** Lederer, 1863:267. (*divitalis* Guenée). Obj. repl. name.
- Glossina* Guenée, 1854:124. (*divitalis* Guenée)
- Pseudocera* Walker, 1863:116. (*inconcisa* Walker).

- Canipsa* Walker, [1866] 1865:1217. (*suspensalis* Walker).
- Matalia* Walker, 1866:1727. (*conci-sella* Walker).
- Phialia* Walker, 1866:1736. (*gelechiella* Walker).
- Sarama* Moore, 1888:203. (*atkinsonii* Moore).
- Scopocera* Moore, 1888:202. (*pyraliata* Moore).
- aeruginosa* Lucas, 1894:155. Australia: Brisbane.
- angulosa* de Joannis, 1929:633. Vitenam: Tonkin.
- angusta* (Inoue, 1988:85) (*Jocara*). Japan: Shizuoka Pref, Nashimoto.
- angustalis* Caradja, 1925:57. China: Lienping.
- asopialis* (Snellen, 1890:568.) (*Pannucha*). India: Darjiling.
- atribasalis* Hampson, 1900:376. Amurland: Sutschau, Askold I.
- atkinsoni* (Moore, 1888:204) (*Sarama*). India: Darjiling.
- atribasalis* Warren, 1895:461. Australia: Queensland.
- leucodesma* Lower, 1896:156. Australia: Queensland: Bulimba, Brisbane.
- basalis* (South, 1901:417) (*Orthaga*). Japan: Nagasaki.
- japonica* (Marumo, 1920:266) (*Lepidogma*). Japan.
- basilaris* (de Joannis, 1929:634) (*Stenicta*). Vietnam: Tonkin.
- bryomima* (Turner, 1913:141) (*Orthaga*). Australia: Queensland, Montville.
- callibrya* Meyrick, 1933:437. Sri Lanka: Batapola.
- caradjai* West, 1931:209. Philippine Islands: Mindanao, Lanao, Kolambungan.
- carbonalis* (Guenée, 1854:77) (*Helia*). Terre de Van-Diemen.
- costigeralis* (Walker, 1862:121) (*Pyralis*). Australia: Sydney.
- gelechiella* (Walker, 1866:1736) (*Phialia*). Australia: Tasmania.
- inuncta* (Lucas, 1898:80) (*Catamola*). Australia: Queensland.
- carneotincta* Hampson, 1896a:123. Sikhim.
- centralis* (Wileman-South, 1917a:129) (*Orthaga*). Formosa.
- conci-sella* (Walker, 1866:1728) (*Matalia*). Australia: Swan River.
- rubroviridis* Warren, 1895:463. Australia: Queensland.
- congenitalis* Hampson, 1906:144. Borneo: Sandakan.
- corticalis* Pagenstecher, 1900:167. Bismarck Archipelago.
- divitalis* (Guenée, 1854:124) (*Glossina*). Central India.
- phereciusalis* (Walker, [1859] 1858:159) (*Locastra*). Borneo: Sarawak.
- dohrni* Hering, 1901:27. Sumatra.
- evanescens* Butler, 1887:115. Solomon Islands: Alu.
- flammealis* Kenrick, 1907:72. Papua New Guinea: Ekeikei.
- hoenei* Caradja and Meyrick, 1935:28. China.
- ignebasalis* Hampson, 1916a:148. New Guinea: Fak-fak.
- inconcisa* (Walker, 1863:116) (*Pseudocera*). Borneo: Sarawak.
- indistincta* Rothschild, 1915:115. New Guinea: Utakwa River.
- lactealis* Caradja, 1931:206. China: Kwanhsien.
- leucozonalis* Hampson, 1906:142. Singapore.
- lophocepsalis* Hampson, 1906:144. Borneo: Sandakan.
- loxochlaena* Meyrick, 1938:74. West Java: Mt. Guntur, Garoet.
- loxophaea* (Turner, 1937:75) (*Epipaschia*). Australia: Queensland, Cape York.
- mediovialis* Hampson, 1916a:148. Queensland: Cairns.
- olivialis* Hampson, 1903:36. Bhután: Khásis.
- orchidivora* (Turner, 1904:199) (*Orthaga*). Australia: Queensland, Burpengary.
- phanerostola* Hampson, 1916a:148. New Guinea: Babooni.
- plumbifloccalis* Hampson, 1896a:123. Burma: Tenasserim.
- prasina* Warren, 1895:462. Australia: Queensland.
- pyraliata* (Moore, 1888:202) (*Scopocera*). India: Darjiling.
- rufescens* Hampson, 1896a:120. Bhután.
- kiiensis* (Marumo, 1920:266) (*Lepidogma*). Japan.
- rurealis* Kenrick, 1912:548. New Guinea: Arfak Mts.
- sectilis* Hering, 1901:21. Sumatra.
- sinuosa* (Moore, 1888:203) (*Scopocera*). India: Darjiling.

- subviridalis* Kenrick, 1907:73. Papua New Guinea: Kebea, Dinawa, Babouni.
- klossi* Rothschild, 1915:115. New Guinea: Utakwa River.
- suspensalis* (Walker, [1866] 1865:1217) (*Canipsa*). Borneo: Sarawak.
- capnotila* (Meyrick, 1938:73) (*Macalla*). South Central Java: Djokjakarta.
- Teliphasa** Moore, 1888:200. (*orbiculifer* Moore)
- albifusa* (Hampson, 1896a:113) (*Macalla*). Sikhim. Nagas.
- shishana* (Strand, 1919:51) (*Macalla*). Taiwan: Shisa.
- andrianalis* Viette, 1960a:158. Madagascar Est: Sakaraha, Lambomakan.
- dibelana* Ghesquière, 1942:238. Zaire: Bena-Dibele.
- nubilosa* Moore, 1888:201. India: Darjiling.
- orbiculifer* Moore, 1888:201. India: Darjiling.
- sakishimensis* Inoue and Yamanaka, 1975:100. Japan: Mt. Banna, Ishigakijima, Ryukyu Is.
- Termioptycha** Meyrick, 1889:504. (*cyanopa* Meyrick)
- Pseudolocastra* Warren, 1891:429. (*inimica* Butler)
- Sialocytara* Turner, 1913:134. (*erasta* Turner)
- aurantiaca* Janse, 1931:455. New Guinea: Arfak Mts.
- bilineata* (Wileman, 1911:364) (*Macalla*). Japan: Settsu, Shioya.
- eucarta* (Felder & Rogenhofer, 1875:pl. cxxxvi, fig. 28) (*Ethnistis*). Moluccas.
- cyanopa* Meyrick, 1889:505. New Guinea.
- erasta* (Turner, 1913:134) (*Sialocytara*). Australia: Queensland, Kuranda.
- distantia* Inoue, 1982:378. Japan.
- inimica* (Butler, 1879b:448) (*Locastra*). Japan.
- elegans* (Butler, 1881:581) (*Locastra*). Japan: Yokohama.
- margarita* (Butler, 1879a:66) (*Locastra*). Japan: Yokohama.
- lativitta* (Moore, 1888:199) (*Locastra*). India: Darjiling.
- nigrescens* (Warren, 1891:428) (*Parasama*?). Japan: Yesso.
- scoparialis* (Wileman, 1911:365) (*Macalla*). Japan: Nikko.
- chosenalis* (Shibuya, 1927b:93) (*Macalla*). Korea.
- Titanoceros** Meyrick, 1884a:62. (*cataxantha* Meyrick)
- cataxantha* Meyrick, 1884a:63. Australia: New South Wales: Sydney.
- heliodyras* Meyrick, 1933:436. Australia: Queensland, Townsville.
- malefica* (Meyrick, 1934:531) (*Jocara*). India: Madras: Nilambur.
- mirandalis* (Caradja, 1925:51) (*Jocara*). China: Lienping.
- poliochyta* Turner, 1904:191. Australia: Queensland, Townsville.
- thermoptera* (Lower, 1903:59) (*Jocara*). Australia: New South Wales, Broken Hill.
- vinotinctalis* (Caradja, 1928:361) (*Jocara*). China: Lienping.
- viridibasalis* (Caradja, 1932:9) (*Jocara*). China: Omei shan.
- Trichotophysa** Warren, 1896:456. (*olivalis* Warren)
- juncundalis* (Walker, 1865:1164) (*Bleptina*?). Sri Lanka.
- olivalis* Warren, 1896:457. India: Khasias.
- olivalis* (Wileman, 1911:365) (*Stericta*). Japan: Yoshino, Yamato.
- yamatomis* (Strand, 1919:55) (*Stericta*). Taiwan: Yamato.
- Incertae sedis**
- africalis* (Hampson, 1906:128) (*Pococera*). Kenya: Tana R.
- cinerea* (Ghesquière, 1942:234) (*Tioga*). Zaire: Elisabethville.
- aethlea* (Ghesquière, 1942:234) (*Tioga*). Zaire: Elisabethville.
- zophoptera* (Ghesquière, 1942:234) (*Tioga*). Zaire: Manghay.
- albicristata* (Warren, 1911:28) (*Isolopha*). South Africa.

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TECHNICAL COMMENTS

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COMPARISON OF BUTTERFLY DIVERSITY IN THE NEOTROPICAL AND ORIENTAL REGIONS

Heppner (1991) admirably compiled and tabulated an immense amount of Lepidopteran diversity data that potentially will be of interest to biologists and conservation policy makers. For example, he concluded that the Oriental Region has more species of Lepidoptera per unit area than the Neotropical Region and stated "... figures of species richness and diversity per unit of land area give a more meaningful understanding of the average loss to be anticipated as each section of land is deforested. ..." The purpose of this note is to alert conservationists and others that the conclusions and numbers in Heppner's paper need to be viewed with caution. Errors range from technical (he used 1.67 to convert mi^2 to km^2 [2.59 is the correct factor]) to logical (see below). Specifically, I show that the variable "species/area," as calculated by Heppner, is not valid for comparing different sized areas, that the numbers of butterflies tabulated in his paper are inconsistent with other published work, and that the Neotropical Region has more than twice the butterfly species for a given area than does the Oriental Region.

IS HEPPNER'S ARGUMENT LOGICAL?

Heppner's argument is simple. The Neotropical Region has 46,313 Lepidoptera species and an area of 7.202 million mi^2 (=18.65 million km^2), whereas the Oriental Region has 26,794 Lepidoptera and an area of 3.934 million mi^2 (=10.19 million km^2). Dividing, the Neotropics have 6434 species/million mi^2 , and the Orient has 6782 species/million mi^2 . From these numbers, Heppner concluded that the Oriental Region has a higher species diversity of Lepidoptera. Using Heppner's method and data for just butterflies, the Neotropical region is barely more diverse than the Oriental Region (1101 vs. 1057 species/million mi^2).

I use a *reductio ad absurdum* argument to show that it is illogical to use "species/area" to compare different sized regions. Approximately 113 species are recorded in Massachusetts (21,386 km^2) while there are about 3130 species in Brazil (8,483,571 km^2) (Opler & Krizek 1984, Brown 1991). Following Heppner's method of comparison, the average diversity of butterflies per unit area in Massachusetts (5.3 species/thousand km^2) is more than 14 times greater than that of Brazil (0.4 species/thousand km^2), which has the highest (or just about the highest) number of butterfly species in the world (Brown 1991).

It is reasonably well-established that species number within a region is a power function of area with the exponent usually in the 0.1–0.4 range (MacArthur & Wilson 1967, Legg 1978, Gilbert 1984). As a result, "species/area" is inversely correlated with area; the larger the area within a region, the smaller the ratio "species/area." Comparisons between areas in different regions depend upon both size and species richness of the two areas. If the sizes are different, the comparison is invalid. This is the case for the example with Massachusetts and Brazil, as it is for Heppner's comparison of the Orient with the much larger Neotropics. A valid comparison requires assessing species number as a function of area within each region (see below).

COMPARISON OF HEPPNER'S TABLES WITH OTHER PUBLISHED SOURCES

To assess the accuracy of Heppner's tables, I examined his species numbers for butterflies. They appear to be biased. His 19,238 butterfly species in the world is 11% higher than the corresponding figure in Shields (1989), 7% higher than that in Brown (1991), and above the range given in Robbins (1982) for described and undescribed species. His figure for butterflies without HesperIIDae is greater than the interval in Ehrlich and Raven

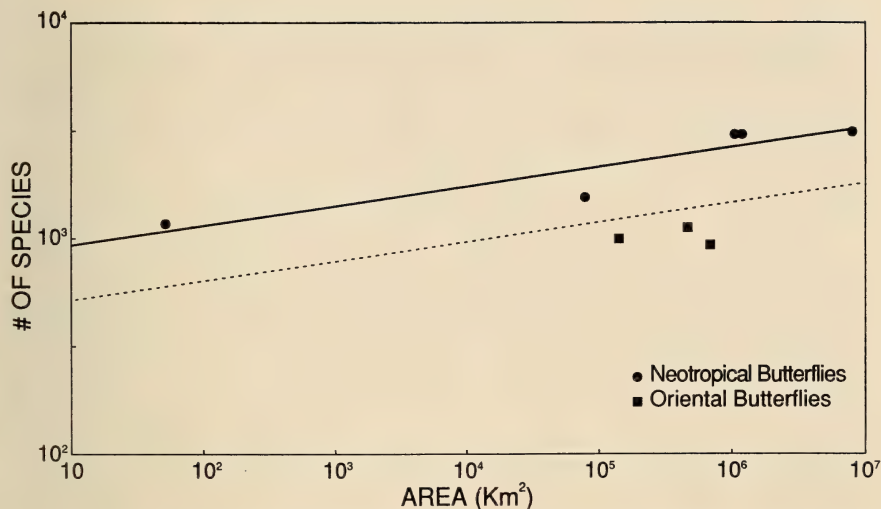


FIG. 1. Log-log plot of species richness in the Neotropics (from left to right, Tambopata, Panama, Colombia, Peru, Brazil) and in the Orient (from left to right, Malay Peninsula, Thailand, Borneo). See text for sources. Solid regression line calculated from Neotropical data. Dotted line represents half the species richness expected in a Neotropical region, showing that Oriental species richness is less than half that of the Neotropics for equal-sized areas.

(1965). Numbers in the table are uniformly higher for families than those in Shields. Heppner's figure for Neotropical Nymphalidae is 42% (almost 850 species) higher than the 2019 species in the Atlas of Neotropical Lepidoptera checklist (Lamas in prep.). Unless documentation is forthcoming for the apparent high bias in Heppner's tables, the butterfly parts should not be used for diversity studies.

NEOTROPICAL VS. ORIENTAL BUTTERFLY DIVERSITY

A comparison of species richness in the Neotropical and Oriental Regions is of biological and conservation interest. Since Heppner's data are insufficient for a valid comparison, I compare these regions using butterflies, for which there are reasonably accurate data. For the Neotropics, I use species richness of the Tambopata Reserve in southeastern Peru (Lamas 1985, Lamas et al. 1991), Panama (Robbins 1982), and Colombia, Peru, and Brazil (Brown 1991). These areas comprise a large portion of the Neotropics, including desert, grassland, scrub forest, rain forest, cloud forest, and paramo habitats. For the Oriental Region, I use diversity in Thailand (Pinratana 1988), the Malay Peninsula (Corbet & Pendlebury 1978), and Borneo (Otsuka 1988, Maruyama 1991, Seki et al. 1991). I do not know of any other reasonably complete, recently published butterfly data from these regions. I plot data on a log-log graph (Fig. 1) and draw a regression line through the points for the Neotropics. Legg (1978) performed a similar analysis, but much of his data differs markedly from that in the publications cited above.

Neotropical butterfly richness is more than twice as great as that in the Orient (Fig. 1), in contrast to the slight difference in Heppner's paper. Extrapolating from the regression line, for example, a Neotropical country the size of Thailand would have 2.2 times the number of species that occur in Thailand. Single collecting sites in the Neotropics (Emmel & Austin 1990; Fig. 1) may have more species than the entire Malay Peninsula or Borneo. In lieu of more complete published data—with which the validity of the power function model could be tested—the Neotropics are richer than the Orient for butterflies, in accord with previous comparisons using less data (Robbins 1982, DeVries 1987). The Neotropics

also appear to be richer for vertebrates and canopy tree species (Gentry 1988). Whether this pattern also holds for other Lepidoptera is unknown, but Sphingidae and Saturniidae are probably the only groups that are sufficiently well-known for a valid comparison.

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RESPONSE TO "COMPARISON OF BUTTERFLY DIVERSITY IN THE
NEOTROPICAL AND ORIENTAL REGIONS" BY ROBERT K. ROBBINS

Robbins' review of Heppner (1991) utilizes one exceedingly small piece of the work (i.e., paragraph 4 on page 4 and Table 4) as a platform to criticize the purpose and logic of the entire study. In doing so, he misses the broader view of the paper—comparisons of Lepidoptera diversity, distribution, and endemism throughout the world. Robbins uses his knowledge of butterflies (15% of the Lepidoptera) to criticize the results of my studies based on all families of Lepidoptera.

Robbins' major criticism focuses on my conclusions regarding species richness. Obviously, taking any small area of the world (like Massachusetts) and using the resultant skewed figures for *extrapolated* species richness comparison is an absurd exercise, and this forms the basis of his criticism. Although Robbins is correct that I am not comparing areas of *equal* size (even areas of equal size may not be comparable because of shape), I am evaluating areas of *comparable* size, i.e., large continental masses of several million square miles. It is clearly stated in my work that the species richness values represent "species per million square miles."

Robbins uses relatively small areas like southeast Peru (Tambopata Reserve) and Rondonia (Brazil) as examples to imply that all the Neotropics are vastly more species rich than the Oriental Region, ignoring the immense Patagonian Plains, the extensive high Andean regions, and the desert regions of Chile and Mexico, where species diversity is very low. If samples from these localities were incorporated into Robbins' species/area regression, they likely would change the regression line and invalidate many of his conclusions. My species/area values are averaged over the total continental landmasses involved. Robbins even corroborates my calculations that there are more species per million square miles in the smaller Oriental Region (6782) than in the vast Neotropical Region (6434). These figures do not diminish the importance of preserving species-rich areas in the Neotropics (I clearly indicate that "the Neotropical region has many more species than any other faunal region"), they only highlight the conservation needs of the much more deforestation-pressured Oriental areas.

Robbins also criticizes my species numbers for butterflies, relying primarily on other published numbers (i.e., Ehrlich & Raven 1965, Robbins 1982, Shields 1989, Brown 1991). He fails to recognize that estimates presented in these works chronologically approach the numbers I presented, i.e., together, previously published estimates of species numbers present a well defined trend in which the estimates increase chronologically along with our increased knowledge of the groups involved. Further, Robbins does not take into account the numbers of species to be described in the future.

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GENERAL NOTE

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AGLAIS URTICAE (NYMPHALIDAE): A NASCENT POPULATION IN NORTH AMERICA

Additional key words: introduction, Eurasian, *Urtica dioica*, New York.

Aglais urticae (Linnaeus), the small tortoiseshell, is one of Europe's most widespread and well-known butterflies (Thompson 1980). It was reportedly collected in the last century in the vicinity of Albany, New York (Emmons 1884), but there is reason to doubt this record (McCabe 1990). A second report was of a male that emerged from a crate of books shipped from England to Halifax, Nova Scotia (Scott & Wright 1972). Most recently, an individual of this species was collected in downtown Albany, New York on 19 October 1987 (McCabe 1990).

On 31 August 1988, two rangers of the Jamaica Bay Wildlife Refuge (a unit of Gateway National Recreation Area) in Queens, New York, noticed an unusual butterfly nectaring at bouncing bets (*Saponaria officinalis*) near the park headquarters. The butterfly, an *A. urticae*, was netted, photographed by Don Riepe, and released. It remained in the area and was seen again on 2 September 1988.



FIG. 1. *Aglais urticae* at the Jamaica Bay Wildlife Refuge, Queens, New York, 25 August 1991. Photograph by Don Riepe.

On 15 October 1990 an individual of *A. urticae* was observed at Riverside Park in Manhattan, New York (Nick Wagerik, pers. comm.). The extensive flower gardens in this park attract many late season southern immigrants. Although the butterfly was not photographed, it was studied carefully at close range with binoculars, thus confirming its identity.

On 25 August 1991 another individual was observed at the Jamaica Bay Wildlife Refuge. This individual was seen by a number of people including Steve Walter, John Zuzworsky, and Don Riepe who again was able to secure a photograph (see Fig. 1).

These sightings could represent independent introductions of this butterfly into the United States but this seems unlikely. A large number of individuals of this species is likely to be present in the Hudson River Valley in order to produce four sightings in five years by the relatively few observers covering this large area. A simpler explanation is that *A. urticae* has colonized the Hudson River Valley and surrounding area. The larval foodplant of *A. urticae* in Eurasia is stinging nettle (*Urtica dioica* var. *dioica*; Urticaceae) (Dal 1982, Henriksen & Kreutzer 1982, Thompson 1980, Brooks & Knight 1982) which is now established throughout the northeastern United States (Gleason & Cronquist 1991).

Aglais urticae is known to overwinter as an adult, sometimes indoors (Dal 1982). A related species of nymphalid has been reported to sometimes overwinter communally (Proctor 1976). Thus it is plausible that a gravid female, or a male and a female together, were introduced accidentally into the United States. North America may prove to be fertile territory for this butterfly.

Two other well-known Eurasian species of butterflies have become established in North America. *Pieris rapae* (Linnaeus) (Pieridae), the cabbage white, was first found at Quebec in 1860 and at New York in 1868 (Scudder 1889). From these beachheads it rapidly spread across North America (Scudder 1889) and is now perhaps our most ubiquitous butterfly. *Thymelicus lineola* (Ochsenheimer) (Hesperiidae), the European skipper, was first recorded in North America from London, Ontario, Canada in 1910. It now occurs abundantly over much of the northeastern United States and adjacent Canada as well as in British Columbia (Burns 1966). For both of these species, the exact manner of introduction is unknown.

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BOOK REVIEWS

THE DEVELOPMENT AND EVOLUTION OF BUTTERFLY WING PATTERNS, by H. Frederik Nijhout. 1991. Smithsonian Institution Press, Washington and London. xvi + 297 pp., 159 figures, 8 color plates. Hard cover (ISBN-0-87474-921-2), \$45.00; soft cover (ISBN-0-87474-917-4), \$20.00; 18 × 26 cm.

Because they are diverse and easy to observe, not to mention beautiful, butterfly wing patterns provide an excellent opportunity for pursuing questions about the development and evolutionary history of morphological patterns. Certainly there are few contemporary scientists who have exploited this potential more than H. Frederik Nijhout. His recent book, *The Development and Evolution of Butterfly Wing Patterns*, summarizes his work and ideas, and makes clear his valuable empirical and theoretical contributions. Butterfly wing patterns are the material theme of this book, which offers a unique and thorough compilation of the existing information on this topic that will be useful for a long time. The conceptual theme is homology and it is in this arena that the book does less than it could. I will begin with an overview of the book and then deal with the concept of homology and how it is handled by Nijhout.

The book is attractively constructed and priced and begins with a nice chapter that summarizes butterfly wing structure and explains pattern production mechanisms. The next three chapters (about a third of the book) are devoted to describing a set of proposed homologies for the diverse pattern elements found both within and between species of butterflies. This set is known as the nymphalid ground plan and is an update of schemes initially proposed independently by Schwanwitsch and Süffert in the 1920's. Chapters 5-7 are devoted to presenting empirical and theoretical results on the developmental and genetic mechanisms that control wing pattern in butterflies. The book concludes with a chapter on the extent to which mechanical and developmental constraints might influence the evolution of butterfly wing patterns, followed by three appendices, a bibliography, and an index. While I realize that the intended focus of this book is butterfly wing patterns, this is to the near and unfortunate exclusion of discussion of studies of homology in the color patterns of other insects or vertebrates.

Copiously illustrated, the book has almost 160 figures and all are crisp and clear. However, many are large and detailed showing numerous pattern variants. The most extreme figure (2.21) shows 110 different shapes found in the parafocal elements among the nymphalids. Similarly, the text contains many lengthy and subjective descriptions and interpretations of specific cases, instead of concise, quantitative summaries and analyses of the observed patterns of variation. This does not make for easy reading or for ready assessment of the support for Nijhout's points.

The nymphalid ground plan is best understood as an hypothesized set of homologies for the similar pattern elements found on butterfly wings both within and among species. Now, what does it mean to a biologist to say that two traits with some common features are homologous? This question has been debated in an extensive and still growing literature since the comparative anatomist, Richard Owen, first proposed the term in the mid-1800's. To most modern evolutionary biologists homology suggests that the similarity in traits reflects similarities in the developmental pathways producing the traits as well as a common ancestry. Hence, to say that two pattern elements that are similar are homologous is to say that they arise by similar processes during development and that they both arose from the same ancestral pattern element. An alternative explanation is that the similarity in the pattern elements is a result of convergent evolution of traits with different developmental and evolutionary antecedents.

Despite the central place of homology in this book and the extensive discussion of this term in the literature, Nijhout spends only a single paragraph explicitly dealing with what he means by homology. His preferred definition, put forth by H. V. Roth in 1984, is that homologous traits need only share a developmental pathway. In his view, issues of the common evolutionary history of homologies are secondary and not a necessary part of the definition. I think most phylogeneticists would regard common evolutionary

history as an essential criterion for homology. Even H. V. Roth suggests that the shared developmental pathways of homologous traits are "controlled by genealogically related genes" (p. 13, 1984, *Biological Journal of the Linnean Society* 22:13–29). The stated definition notwithstanding, it is clear throughout the book that the evolutionary past frequently figures prominently in Nijhout's recognition of homologies.

But Nijhout seems at times a little cavalier in his application of his preferred definition. In his discussion of experiments on forewing and hindwing eyespots, he concludes that, "we can be as certain about their homology across butterflies as we can about any system of homologies in the animal kingdom. Yet the processes that give rise to these two types of eyespots appear to be different. . . ." (pp. 113–114). In the discussion that follows, this statement is justified by the citation of an alternative criterion for homology proposed by Van Valen: continuity of developmental information. However, Nijhout does not make clear what general conditions make appropriate the use of this criterion versus some other. Again, I think the book would have benefitted greatly from a full discussion of Nijhout's views on the concept of homology, its definition, and application.

Although Nijhout points out that the ground plan is not to be taken as a putative ancestral coloration for butterflies, the ground plan homologies can be taken as an hypothesis of shared developmental pathways and common ancestry. Such an hypothesis can be tested in two ways. One way is to generate predicted phylogenetic relationships among the species within groups of butterflies. These predictions derived from wing patterns can then be tested for concordance with phylogenies developed from other characters, e.g., wing venation, DNA sequences, etc.

Nijhout makes a cogent and well-taken plea for systematists and phylogeneticists to use and test the ground plan in this way. In Chapters 3 and 4, Nijhout offers a number of phylogenetic relationships within various genera that are predicted by the nymphalid ground plan. However, Nijhout could have improved the case for the ground plan if he had provided some clear tests of the phylogenies proposed by the ground plan. As the presentation stands many questions remain. What other systems of homologies and resulting phylogenies have been proposed or examined? How and why were they rejected? Does the nymphalid ground plan permit one to construct phylogenies that are concordant with those from other data? What taxonomic issues have been or might well be resolved using the homologies hypothesized in the ground plan? Are there other taxa in which study of pattern homologies have helped resolve taxonomic and phylogenetic issues?

Relevant to the issues of taxonomy the book contains an Appendix by Donald J. Harvey entitled "Higher Classification of the Nymphalidae." In it Harvey presents a *newly revised* classification for the nymphalids between the level of family and genus. Its inclusion in this book seems odd on two counts. First, although Harvey acknowledges the input of some very able reviewers, the precise review process through which this classification has gone is unclear. Does the revised classification (published as an appendix) have the same standing as a paper published through regular journal review processes? Second, its precise relevance to the rest of the book is unclear in that it is rarely referenced by Nijhout and does not use the nymphalid ground plan to resolve any taxonomic or phylogenetic issues in the way Nijhout suggests in Chapter 4.

The other way to test a set of homologies such as the nymphalid ground plan is to see if the pattern elements proposed to be homologous in fact share developmental pathways and genetic control mechanisms. Results from manipulation (Chapter 5) and genetic (Chapter 6) experiments and a model for wing pattern development (Chapter 7) are described in detail but not with the explicit purpose of testing the ground plan in this way. Here as elsewhere in the book the ground plan is presented more as a given and not as a tentative and testable hypothesis. Nijhout does conclude that his work and that of others show that a seemingly limitless diversity of patterns can be produced by slight changes in the location and shape of inductive signal sources and sinks, in the thresholds of responding cells, and in the genes controlling pattern.

Two other salient features of the ground plan should be mentioned. First, the plan does not homologize the color of pattern elements, but only their position, shape, and presence. Nijhout points out that two identical pattern elements can look very different if colored in different ways. What potential information about development and evolution

is omitted by not fully incorporating the variable of color into the system of homologies? Nijhout provides no specific answer to this question. Second, the plan is subjective in that there is no effort to quantify the similarities between pattern elements that lead to a hypothesis of homology. In general the lack of quantification in the description of pattern elements and in efforts to test Nijhout's ideas is notable.

The last chapter speculates on the impact of developmental or phylogenetic constraints and selection on the evolution of butterfly coloration. There are two key conclusions. First, many of the features of pattern elements (e.g., the shape of small elements such as parafoveal elements) are probably not under direct selection and their evolution will be determined by what sort of pattern production mechanisms are available. This view seems plausible but highly speculative in that it broadly assumes interspecific similarity in the features of the visual system of predators and in the contexts of encounters. Second, the pattern-generating systems are so flexible that the evolutionary paths along which butterfly wing pattern may travel, driven by selection or other processes, are virtually limitless. This is good news for adaptationists whose hypotheses are often criticized for assuming few if any constraints on the trajectories evolution can take.

In summary, this book stands as a clear and current record of Nijhout's ideas and of his view of his and others' work on the evolution and development of butterfly wing patterns. It is unique and of interest as a treatise on phylogenetic and developmental questions about these wing patterns. However, the reader must keep in mind that Nijhout presents only a single hypothesis for the inter- and intraspecific similarities in butterfly wing patterns and that the test of this hypothesis is incomplete. My hope is that researchers in this area will be stimulated by the challenge of generating and testing new sets of homologies as alternatives to the nymphalid ground plan.

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A FIELD GUIDE TO EASTERN BUTTERFLIES, by Paul A. Opler (illustrated by Vichai Malikul, with foreword by Roger Tory Peterson). 1992. Peterson Field Guide Series, No. 4. Houghton Mifflin, Boston. xvii + 396 pp., 541 color paintings, 104 color photographs of living insects, and 348 range maps. Hardcover, 12 × 19 cm, ISBN-0-395-36452-3, \$24.95; softcover, 11.5 × 18 cm, ISBN-0-395-63279-X, \$16.95.

Was a new eastern field guide necessary? The total of 422 species described by Alexander B. Klots in his original guide in 1951 has expanded to 524 species, through the recognition of many more occasional immigrants and the addition of a few recently described species, minus a few species submerged to subspecies status. With this, and the acquisition of much new biological information, forty years was not too soon for an update.

The browser picks up this new field guide, turns to the color plates to see how the butterflies look, and sees—flowers! Thereafter follow three pages of photos of immature stages: first things first. And now nine pages, 68 superb photographs, of living butterflies doing what we most enjoy seeing them do: nectaring, basking, puddling. Their characteristic postures are clearly evident. Finally, on 35 color plates we see the expected formally sequenced, conventionally spread depictions of the great majority of the 524 species covered in the book, as color paintings ranging from superb (most of them), to barely adequate (only a few: i.e., in the genus *Erynnis*—but *Erynnis* are the *bêtes noires* of most lepidopterists).

By using this sequence, Opler is subtly emphasizing points made in his introductory chapters: the dependence of butterflies on their botanical substrates, and the fact that users of this book who wish to observe and photograph butterflies will greatly outnumber those who make collections of specimens. While acknowledging changing attitudes and

interests with regard to invertebrates, he does not in any way denigrate collecting. In fact, he describes in careful detail, with clarifying line drawings, the collecting and preservation of specimens, with emphasis on proper and purposeful collecting, and on responsible care of collections. The necessary information about butterfly anatomy, development, and behavior is well covered, as are rearing, gardening for butterflies, butterfly conservation, and in particular, life zones and butterfly habitats.

By whatever magic, Opler has succeeded in an area where his field guide predecessors were constrained: Klots with the original *Field Guide to Eastern Butterflies*, C. V. Covell with the *Field Guide to the Moths of Eastern North America*, and W. Tilden and A. C. Smith with the *Field Guide to Western Butterflies*. The illustrations of all the butterflies, even the black and white ones, are in color, thereby increasing the appeal and usefulness of the guide. And he has regained the benefits of "triple-indexing," e.g.: White, Checkered, *Pontia protodice*, *protodice* (*Pontia*). The reader accustomed to finding *protodice* in *Pieris* will nevertheless find the species readily in this index.

The color values, fine detail, and general *gestalt* of most of Malikul's paintings are magnificent. One could only wish that this were not a field guide, so that all species might have been portrayed at life size. This, in fact, is the basis of a minor problem. It is immediately obvious that the stated scale for many plates must be taken with a grain of salt. In Plate 16, for example, at the stated scale of $\times \frac{1}{2}$, *canadensis* and *glaucus* are portrayed the same size, yet *glaucus* is rarely as small as *canadensis* and often is twice as large. On the same plate *rapae* is shown slightly larger than $\times \frac{1}{2}$ so that it seems almost to match the span of *glaucus*. And Plate 32, with various brushfoots, measures out at close to $\times \frac{1}{2}$, rather than the stated $\times 1$. The caveat (Lepidoptera or no): go by the text, not by the scales!

This reader often approaches a new guide with an element of anxiety: "What names will they use *this* time?" Opler has opted for the conservative stance he employed in *Butterflies East of the Great Plains* (with George O. Krizek, 1984, The Johns Hopkins University Press, Baltimore, 294 pp.). He has even abandoned *Polites coras* in favor of *P. peckius*, familiar from Klots and from W. J. Holland (1898, *The Butterfly Book*, Doubleday, Page & Company, Garden City, NY, 382 pp.). But it was not an easy victory: Peck's Skipper is *P. coras* on Plate 13, *P. peckius* on Plate 44. When even the experts can get trapped in habit, it makes the dilemmas of nomenclature a little less tense for the rest of us!

The decision to avoid dwelling heavily on subspecies was a good one for a field guide to eastern North America, where subspecies rarely have sharply definable ranges. The "Life List" clearly points out which subspecies are actually found within the study area, and which of the nominate subspecies are extralimital. This, however, has introduced another minor problem. One would wish that the common name selected for each species were regularly that of the subspecies found within our area, such as American Copper (rather than Little Copper) for *Lycaena phlaeas americana*, or Tropical Buckeye (rather than Genoveva) for *Junonia genoveva zonalis*. The most disconcerting subspecies problem arose with Evans' Skipper, *Panoquina fustina evansi*. It is properly described in the species account as having a "vague irregular white postmedian band." The plate, however, illustrates the nominate (extralimital) *fustina*, which bears a strikingly clear broad white band.

Species accounts are in the Klots (and Opler) tradition, covering color, pattern, shape, size, pleomorphism, and polyphenism. Similar species are compared; early stages, larval host plant, flight period are covered when known; diapausal stage is stated individually or by genus or large group, as applicable. This, coupled with the range (there are range maps for most resident species) and habitat information, provides a valid basis for searching for a species in the field, or identifying a specimen on film or in hand. A "remarks" section, for some species, gives significant behavioral and historical details. Genitalic details are not described, but their importance is stated for those species where they are critical for correct determination.

A recurring theme surfaces in the species accounts, as for example the following for *Nastra lherminier*, the Swarthy Skipper: "Early Stages: Not reported. Food: Little Blue-stem." This opens up a gold mine of opportunity for the amateur lepidopterist: the

challenge of rearing, describing, and reporting early stages, so that the many lacunae in the knowledge of immatures can be gradually filled in. And for many other species Opler indicates that the larval host plant is still unknown. Field observations can provide the answers. Such information is essential for the understanding of the environmental requirements of threatened or endangered species.

There are scattered and sometimes confusing inconsistencies relating to diagnostic arrows, plate labels, and the explanatory captions accompanying the plates. A plate figure labelled as male may indeed be female, and properly described as female. Rarely a plate figure is unlabelled, or improperly labelled. A diagnostic arrow may point to a feature not referred to in the caption or species description, or an arrow may significantly miss pointing out the designated feature. Occasionally a range map may not coincide with the verbal account of the range. While these inconsistencies may at times be confusing to the novice, they usually can be worked out by careful comparison of the text in the plate caption with that in the species description. Such flaws are by no means insurmountable and should be readily correctible in a second printing. Incidentally, the Palatka Skipper (*Euphyes pilatka*) is not a typo: there probably was a slip-of-the-pen by W. H. Edwards in the mid-nineteenth century when he described the creature.

With the completion of the species accounts, the author devotes the remaining fifteen percent of the book to extremely useful accessory material. A "Life List" follows the sequence of the Miller and Brown list, except that the skippers are placed after the "true" butterflies, as in the body of the guide. There is a contingent benefit from this: the skippers present a challenge that the novice may prefer to defer. To have placed them first might have diminished the appeal of the book for some; swallowtails, on the other hand, are an immediate attraction. The list ends with a selection of nearly thirty "potentials," species almost reaching the covered area that have a good chance of wandering across the line, or of being accidentally introduced by the increasing agricultural commerce with the southern part of the hemisphere.

A copious glossary clarifies terms used in the introductory material and in the species accounts, making prior knowledge of lepidopteral terminology unnecessary for full enjoyment of the book. A list of references gives the reader access to general books on identification, butterfly biology and behavior, as well as state or more local coverages and checklists. The several very helpful books on butterfly gardening are not included, however. There are extensive directories of organizations devoted to Lepidoptera, of suppliers of books and equipment, and of butterfly houses and insect zoos. The Collecting Guidelines formulated by The Lepidopterists' Society in 1982 constitute the final appendix. The indices, one for plants, one for butterflies, are exceedingly effective. The internal indexing between plate and text greatly simplifies use of the book.

In summary, the long-awaited and much-needed update of the Klots Field Guide is now here. Opler's species accounts, in the manner of those he pioneered in *Butterflies East of the Great Plains*, but necessarily condensed, provide the basic framework with which to establish acquaintance with any of the species of eastern butterflies, and from which to pursue further information, known and unknown. The live photos and Malikul's outstanding paintings reduce uncertainties to a minimum. This volume should become the standard resource for the study and enjoyment of eastern butterflies for the next several decades. It has been well worth waiting for.

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THE COMMON NAMES OF NORTH AMERICAN BUTTERFLIES, edited by Jacqueline Y. Miller (Foreword by Paul A. Opler). 1992. Smithsonian Institution Press, Washington, D.C. ix + 177 pp. Soft cover, 15 × 23 cm, ISBN-1-56098-122-9, \$14.95.

History first, though I lift quite directly from R. M. Pyle (1984, *J. Res. Lepid.* 23:89-93). When Robert Michael Pyle produced the *Audubon Society Field Guide to North American Butterflies*, the editors required him to furnish vernacular (common) names for every entry. Since some species had no common names, he had to invent some. Many included were nowhere in use and plenty of them carried little or no biological information. Disturbed by these problems and certain that other authors would also be required to make their own choices or inventions of common names, Pyle proposed the formation of a Common Names Committee, jointly between the Xerces Society and the Lepidopterists' Society. A committee of 20 members was formed by 1984. The committee was to collect published and proposed vernacular (English) names and recommend a list of standard names. As the work evolved, it was decided to make recommendations only in the less difficult cases, simply listing all published names. No attempt was made to invent more suitable names than those already published.

Upon the proposal of a committee, resistance arose, with some basis. Lifting freely from D. Murphy and P. Ehrlich (1983, *J. Res. Lepid.* 22:154-158), the main arguments against doing anything to promote the use of common names were these:

1. Common names lack universality, which the Latinized (scientific) names have.
2. Information content, biological and cladistic, on average is very low.
3. The vernacular languages of common names do not cross most national boundaries.
4. Vernacular names insult the intelligence of the great majority who can easily learn the Latinized names.
5. Common names, when gratuitously provided, act as obstacles to learning the Latinized names that allow entry into the scientific literature.
6. Researching common names and arguing about which name to recommend is a waste of the time of people with important functions related to biological conservation.

Pyle answered these objections effectively, bringing recantation from Murphy and Ehrlich.

1. As J. A. Scott (*News of the Lepid. Soc.* #6, 1985) pointed out (and ornithologists agree: Calvin Hom, pers. comm.), in the case of birds, the common names are in fact more universal than the scientific names. This has occurred because the common names have been standardized while the Latinized names have been repeatedly changed. So long as evolutionary biologists are taken seriously when they change generic names to better match their momentary concepts of the evolutionary relationships of taxa, standardized common names have high potential for exceeding the usefulness of Latinized names to scientist and layman alike.

2. The point that common names carry little information is true, but hardly differentiates them from Latinized names. Every patronym is an assault on the information content of a name, Smith's Blue as much as *smithi*. On this point I stand with Darwin. Common names can be chosen to be non-patronymic, even when the Latinized name is a patronym. *Euphydryas editha luestherae* can be called the Chaparral Checkerspot or the Lousewort Checkerspot, for instance.

3. Within nations, common names will be in local vernaculars, but so long as the language of international conservation remains English, an English common name may be demanded for every Uzbek, French, German, and Chinese species. Having our list in order sooner encourages the rest of the world to conform to our usage.

- 4, 5, & 6. The most telling point: the majority of us who could become interested in biology and conservation of insects tune out the Latinized names, at least at first. Since the media, our link to the public, demands common names we must supply the best ones we can, or lose the attention of the public. The common names act as a link to, rather than as an obstacle to, the Latinized names. Time spent improving and making common names available greatly increases public access to butterfly biology.

The twenty committee members who labored to generate this highly valuable reference work have my sincere gratitude. Authors seeking appropriate common names can now find them. Anyone with information or interest in a butterfly that he or she knows only by a common name can now look it up and see what the Latinized name might be. The public and responding government agencies often raise biological concerns during land-use permitting procedures by common name only. Today I was asked about the "checkered moth" (suggesting a need for more work). The book offers a list of common names collected from all major sources, with a recommended name in boldface for each species. Subspecies and their common names are also listed but none is designated as recommended. Publication of this work will have the instant effect of producing new sources of previously published common names and advice on which of several possibilities to adopt into the standard list. I would mention a real need for separate names for the species and for the nominate subspecies. A second edition should appear, in my opinion, in well under ten years.

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46(4), 1992, 311-313

MOTHS OF AUSTRALIA, by Ian F. B. Common, with photographs by Ederic Slater. 1990. Melbourne University Press, Carlton, Victoria 3053, Australia. Distributed by E. J. Brill (USA), 24 Hudson Street, Kinderhook, New York 12106. 535 pp., 32 color plates, 44 black & white plates. Hard cover, 18 × 25 cm, ISBN-0-522-84326-3, \$150 Australian (about \$200 U.S.).

REVIEW BY J. A. POWELL

This book, the fruit of four decades of labour by an incredibly dedicated lepidopterist, is marvelous. In addition to its usefulness to students of the Australian fauna, this text is the best general reference to biology and taxonomy of world Lepidoptera. The information is comprehensive, with comparable coverage of all taxa from primitive moths to macros; the text is clearly written; and the illustrations, particularly the color plates, are superb.

Moths of Australia is presented in two sections: 1, Moths and Their Environment, and 2, The Australian Moth Fauna. There are appendices on collection and study of Lepidoptera and a larval foods list arranged taxonomically by plants with the moths names but not page references. The index lists moth taxa and general topics but not plant names, and there is a glossary as well as extensive bibliography.

In Part 1 there are discussions of morphology and life history, biology, population control, economic significance, evolution and geographical distribution, and a tabular family classification, that are worldwide in application—an 80-page must reference for every lepidopterist. As an example of the comprehensiveness of coverage, probably more has been published on the systematics, phylogeny, and biology of extinct and extant primitive Lepidoptera during the past 15 years than in all preceding time. Recently, for a review of evolution of larval foods, I compiled more than 80 references since 1978 on primitive taxa and higher classification; virtually all the important ones from all biogeographical regions are included by Common. The literature coverage is thorough to about 1988, with a few 1989 citations.

The classification was prepared in collaboration with E. S. Nielsen and is the system to be used in a forthcoming checklist of Australian Lepidoptera, edited by Nielsen and others. The higher taxa comprise a collapsed Linnaean hierarchical arrangement, with four suborders, and six infraorders within the Glossata, as contrasted with five infraorders treated by Minet (1986, *Alexandor* 14:291) and four by Nielsen (1989, *The Hierarchy of Life*, Elsevier Sci. Publ.). Thus Daconophya, Neopseustina, Exoporia, and Lophocoronina are recognized at the same taxonomic level as Heteroneura and Ditrysia. The Ditrysia is divided into 26 superfamilies (in addition to the skippers and butterflies), without inter-

mediate categories. There is a list of world families of moths, about 40 of which are not known in Australia.

Part 2 treats the Australian fauna and contains summaries of adult, immature stages, and biology of each family, including diagnoses of exemplar species. These accounts are accompanied by more than 400 excellent line drawings done by Common, depicting wing venation, male and female genitalia, and the pupa of one or two representative species in each family. The discussions are clearly and concisely written, mostly 3–7 pages, although more diverse families are given more elaborate treatment, for example 14 pages for Oecophoridae and 26 pages for Noctuidae.

The description of Australian species is dependent in large part upon the photographs, about 750 in color and 700 black and white; the latter are not on high gloss paper but are nonetheless very good. Presumably costs would have been prohibitive to publish all photos in color. About 150 of the color and 75 of the halftone photos are of mines, galls, or living insects, either adult or larva.

The Australian lepidopterous fauna, as is true of other animals, consists mostly of endemic species and is markedly disharmonious in comparison to other parts of the world. It has about 10,500 described Lepidoptera and is estimated to contain an equal number of undescribed species. If so, the Australian continent, which is about the size of the United States, has several thousand more species than does the fauna of America north of Mexico, which we would like to think is 70–75% described. The Oecophoridae dominate the Australian fauna, with more than 2600 described species, a further 1500 known species awaiting description, and a total fauna greater than 5000 species. Common projects, or nearly a quarter of all the Lepidoptera. The primitive moths are well represented, both in higher taxa and their included numbers of species, particularly the many large and spectacular Hepialidae, more so than in most other parts of the world. By contrast, other large moths such as Saturniidae (12 species) and Sphingidae (59 species) are depauperate. Butterflies are negligible in terms of biodiversity, even more so than on other continents, with fewer than 400 species, 2% of the estimated fauna.

Common (1980, J. Lepid. Soc. 34:286) has discussed factors responsible for some of these imbalances. Large sections of the Dityrsia, notably Oecophoridae and Tortricidae, have evolved with the typically Australian dry sclerophyll communities dominated by Myrtaceae (especially *Eucalyptus*), Fabaceae (especially *Acacia*), and Proteaceae. In particular, larval feeding in leaf litter of the eucalypt forests seems to have set the stage for speciation. Largely through Common's efforts during the past 40 years, the larval foods of nearly 1000 species of microlepidoptera are known; among these, 35% of Tortricinae and 83% of Oecophoridae feed on *Eucalyptus*, the vast majority in fallen leaves. Means of 100–440 lepidopterous larvae per m² of leaf litter have been reported!

The text and illustrations emphasize families with larger individuals: nearly half of the 100+ hepialid and 50+ sphingid species and about 10% of 1600+ noctuids are shown. In contrast, it is curious that the groups to which Common has directed most of his taxonomic research are underemphasized: only about 70 Oecophoridae and 25 Tortricidae are illustrated, less than 3% of the described species in these taxa.

After a cursory comparison of unidentified specimens, it appears to me that this manual will be useful in indentifying the majority of larger moths, at least to the generic level, although this might be a naive assumption based on lack of familiarity with the macro families or because incidental collections by foreign visitors are liable to emphasize the more distinctive, showy species. For the larger families of microlepidoptera, however, too few are illustrated to allow much identification use. For example, in Tortricidae just one species of each of seven Tribes of Tortricinae (about 80 genera) and no Olethreutinae are illustrated in color, and only about a dozen olethreutines, including several introduced pest species, appear as halftones. Among Gelechioidea, representatives of 23 of 105 described genera of Cosmopterigidae and Gelechiidae are pictured, and only about 35 of 200+ named genera of Oecophoridae (including Xyloryctidae) and Depressariidae are included in the color plates. Moreover, superficial resemblances among the multicolored oecophorids are apt to be misleading, rendering limited usefulness to the photographs.

Ian F. B. Common, who was president of The Lepidopterists' Society in 1979, was educated in Queensland, and joined the Division of Entomology, CSIRO, in Canberra,

A.C.T., in 1948. Since that time he has dedicated his life to an understanding of the Australian moth fauna, aided immeasurably by his wife Jill, who has kindly assisted Ian in countless ways. This book summarizes much of that wealth of information. Possibly the best endorsement I can offer is, this is the reference I reach for first to answer general questions on biology and taxonomy of the families of moths, despite its emphasis on the Australian fauna, halfway around the world from North America.

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MOTHS OF AUSTRALIA, by Ian F. B. Common, with photographs by Ederic Slater. 1990. Melbourne University Press, Carlton, Victoria 3053, Australia. Distributed by E. J. Brill (USA), 24 Hudson Street, Kinderhook, New York 12106. 535 pp., 32 color plates, 44 black & white plates. Hard cover, 18 × 25 cm, ISBN-0-522-84326-3, \$150 Australian (about \$200 U.S.).

ADDITIONAL COMMENTS BY RICHARD S. PEIGLER

I had not seen this book when I ordered it, but what I received far exceeded my expectations. Given that the microlepidoptera comprise the vast majority of families within Lepidoptera, here at last is a treatment that provides balance, which means that there is more coverage of the "micro" families than of the "macro" families. Taxonomic changes at all levels can be confusing to the non-specialist, so I like the way Dr. Common explains at the beginning of each family treatment the historical classification of subfamily, family, or superfamily by earlier authors. The numerous subfamilies of the Noctuidae are clearly outlined, for example.

Although the museum where I work has very few moths from Australia, this book is already proving to have considerable value in curating the moth collection because of its concise morphological descriptions and drawings for all of the families, particularly the microlepidoptera. Many of the micros that I collect are not immediately recognizable by me to family level, and I am faced with looking in moth books such as C. V. Covell's 1984 *A Field Guide to the Moths of Eastern North America*, W. J. Holland's 1903 *The Moth Book*, faunal treatments I have of southeastern Asia or southern Africa, or even the standard college textbook of entomology with keys to families, i.e., various editions of *An Introduction to the Study of Insects* by D. J. Borror and colleagues. But none of these are really adequate compared to Common's book, which presents everything so clearly and all under one cover. True, a few families and subfamilies are Australian endemics, but if one wishes to gain a good working knowledge of the moth families of the world, I am not aware of a better source. So this book will serve worldwide as a useful reference even to those "up above" who have no material from Australia and who never anticipate collecting "down under."

Moths of Australia is beautifully produced. The binding, printing, and color plates are of the highest standard. There is a generous amount of color and numerous black and white photographs showing eggs, caterpillars, pupae, cocoons, and moths in living repose, as well as pinned adults. This book is not just a compilation based on literature and museum material; Common has obviously spent countless hours in the field over many years enabling him to report first-hand observations throughout the text. The book is regrettably expensive. If you cannot afford it, try to persuade a nearby museum, university, or public library to order a copy, as it deserves to be widely available for many years to come. Books like this encourage young amateurs to move from butterflies to moths, and advanced amateurs to move to microlepidoptera.

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OBITUARIES

ALEXANDER BARRETT KLOTS (1903-1989)

Alexander Barrett Klots sparked, and in some people ignited, a passion for butterflies and moths among generations of naturalists. His published works include a wealth of popular books and articles, natural history literature for young adults, and over 90 peer-reviewed scientific papers, including benchmark contributions on pierid and crambid systematics, lepidopteran genitalia, and the biogeography of alpine and arctic butterflies. To many he was best known for his Peterson Field Guide on eastern butterflies, which made North American lepidopterology accessible to the amateur, young student, and professional alike. Klots passed away on 18 April 1989 at the age of 85. His wife of 61 years, Elsie Broughton Klots, Ph.D., passed away in September 1991; they are survived by their two children, Cornelius Ephraim Klots, Ph.D., and Louise Snell, and four grandchildren.

Alexander Barrett was born 12 December 1903 to Dr. Ephraim and Helen Giles Klots in New York City. His father was a highly respected and successful medical practitioner. His upbringing was formal, and in some respects stifling; indeed, his mother had him wear velvet suits with lace collars. His father gave him the name "Bill"—the name most of us would come to know him by—to add a more common air to his childhood.

Like that of so many naturalists, Bill's interest in the outdoors was apparent from an early age. At the age of nine he presented the entomology department at the American Museum of Natural History (AMNH) with his first significant butterfly capture. By age 12 he was a frequent visitor to the offices of Mr. Frank Watson and Dr. Frank Lutz at the American Museum. This was also the period when he met F. Martin Brown, someone who would be a lifelong friend and fellow lepidopterist. Frank Watson took a liking to both "Barrett" and Martin and encouraged them to work on the pierids in the AMNH.

Bill's interests as a boy and young man included fishing and bird hunting, rock climbing, scouting, and golfing. He had the "collecting" affliction many of us share; he saved stamps and coins, kept live reptiles and amphibians, and brought home myriad insects. Except for his hobbies of stamp and coin collecting, most of his activities took Bill outside. As a boy he spent countless hours exploring the countryside around the family's summer cottage on Long Island. In 1917, his mother purchased Penhaven, in Putnam, Connecticut, initially to serve as a private retreat. With time, Penhaven became the family summer home, and eventually the homestead to which Bill and Elsie retired.

Bill attended Trinity School in New York City and Blair Academy in New Jersey. From there it was on to Dartmouth to study medicine; evidently he spent too much time in the school's outing cabins and too little time in classrooms. He got a second chance, at Yale, where he finished three years of course work in engineering before leaving to spend a summer working on a dude ranch in Wyoming, an experience that would forever bond Bill to the West. His free time was spent hiking, taking photographs, and collecting insects. He persuaded his father to buy a horse ranch in Jackson Hole with a friend that Bill had met from Lapland. Although he enjoyed ranching, Bill realized that he wanted to get an advanced degree in entomology studying butterfly systematics.

He wrote William T. Forbes and soon was doing graduate work at Cornell University. His Masters research focused on the taxonomy of the pierid genus *Eurema*, the very genus Frank Watson had encouraged Bill to study nearly a decade before. While in the final throes of completing his Masters, it was revealed that young Klots had yet to obtain a Bachelor's degree! Bill, now a dedicated student, quickly had this situation remedied and both degrees in hand. He stayed with Forbes to obtain his doctorate, preparing a generic revision of the Pieridae. While at Cornell Bill met and later married Elsie Broughton, one of Needham's students who was among the first women in the country to complete doctoral work in entomology. Bill and Elsie married in 1927.

Klots graduated in 1931 at the height of the Great Depression, when few universities were hiring. He was offered a very good job in Rochester, New York, at Wards Natural Science Establishment, which was owned by the University of Rochester. Although working there full time, he found time to teach courses at the University of Rochester, where



Alexander Barrett Klots circa 1959 (courtesy Saul Frommer).

he was an associate faculty member. Wards sent Bill out West during summers to collect biological specimens (e.g., insects and fossils), most of which would be sold by the company. He had considerable freedom to pursue his entomological interests while at Wards: he continued publishing on pierid systematics, wrote a widely used manual on how to make an insect collection, and continued his pioneering studies on insect genitalia.

In 1934, Bill was offered a faculty position in the Biology Department at the City College of New York, where he taught courses in biology and field zoology; he also was among the first to offer a course in the new science of ecology. He spent long hours individually tutoring students in entomology, a course that was not formally offered at City College. He made special efforts to get his students outdoors for field trips. Saul Frommer, one of Bill's later students, recalls Klots telling his students that "The ones who jump into the mud with him will get the specimens," almost as clearly as he remembers taking his first leap into a bog with Bill.

Bill was an outstanding lecturer and teacher; his presentations often featured his photographs or other demonstration material he had accumulated. Although City College was an undergraduate institution with relatively few students interested in biological sciences, several of his students went on to other institutions to pursue advanced degrees and careers studying insects, e.g., Fenja Brodo (Nematocera and arctic insects), Herbert Dalmat (Simuliidae), Saul I. Frommer (Curator of Entomology, University of California, Riverside), and Robert Traub (Siphonaptera). The Biology Department at City College was exceptionally strong in entomologists through much of Bill's tenure: William S. Creighton, Axel L. Melander, A. Glenn Richards, Jr., Herbert Ruckes, Herman T. Spieth, and Asher E. Treat, among others. The entomological atmosphere at City College played a part in Bill's decision to decline a job offer from the American Museum of Natural History early in his career. He was named Emeritus Professor upon his departure from City College in 1965.

William Sargeant, a fellow professor and close friend at City College, introduced Bill to the sport of falconry. Klots and a number of other young men spent many weekends



Bill with his pet peregrines.

at Assateague Island, catching or flying birds. Bill, Elsie, and the two children, Ephraim and Louise, kept several falcons, with as many as four in residence in some years. Susana, one of their peregrines, was featured in *Life* magazine; the family favorite was a kestrel named Butch that rode with Elsie in taxis, on trains, and even slept on her pillow.

In 1942 Bill enlisted in the Army Air Force and was commissioned as a Captain in the Troop Carrier Command. After learning of Klots' background in entomology, the army asked him to serve in the Sanitary Corps as a Medical Inspector and Malaria Control Officer. His most noteworthy efforts were his efficacy studies of the new wonder pesticide, DDT, in the control of malaria and yellow fever. He authored three papers documenting the effects of DDT on mosquitoes. He was rather cavalier with DDT use—it was not uncommon to find his clothing dusted white with the powder. One of his former students recalls receiving an envelope that Bill had packed and mailed off to him—Bill urging him to give the new pesticide a try.

Bill's studies took him throughout the southeastern United States, as well as Puerto Rico, British Guiana, and Brazil. His wartime letters to Elsie were censored—the army cut away any mention of places, dates, etc. Bill and Elsie found this most bothersome . . . so they soon devised an interesting way to let each other know his whereabouts—in each letter he would include mention of several butterfly species. Elsie would take these letters to the American Museum of Natural History, where with a little work in the collection, she could pin down his general whereabouts.

Bill met Sergeant Roger Tory Peterson in the army. The two men shared several common interests: both were lifelong naturalists, each had a deep interest in birds, and both were studying DDT. (Peterson was evaluating the impact of DDT on birds.) After the war, Klots became a strong adversary of DDT and other broad spectrum pesticides. His early position of advocacy regarding the use of DDT haunted him . . . it seems most ironic that one of Bill's favorite animals and long time family pet, the Peregrine Falcon, was among the most adversely effected by DDT use. The relationship Peterson and Klots established during the war years led the former to invite Bill to author the field guide on butterflies.

Klots' wartime studies of mosquitoes made him a natural choice for a prestigious Canadian Air Force expedition to the high arctic to study biting flies. Klots spent much of the summer of 1952 studying means for controlling the swarming black fly and mosquito



Clockwise from upper left: Bill (wearing glasses) with Frank Lutz, curator at the American Museum of Natural History, during an informal lecture Lutz presented to a group of Boy Scouts; Klots (back, left) climbing what he coined "Oeneis Mountain" in the Wind River Range, Wyoming, with colleagues from the City College of New York; Klots (center) with his closest lifelong friend, C. F. dos Passos (right) and N. D. Riley (left) at the 1953 International Zoological Congress in Copenhagen; Paul Ehrlich (left) and Saul Frommer (center) and Klots (right) visit at Kansas University, ca. 1959; wartime DDT efficacy studies—Klots samples for adult mosquitoes from an army helicopter.

populations on Ellesmere and Cornwallis islands. He returned at the end of the summer with some 40,000 specimens of *Nematocera*, as well as long series of many arctic butterflies.

Klots' association with the American Museum of Natural History spanned more than 70 years. He kept close ties with Frank Watson and others in the entomology department during his years at Cornell and later at Rochester. After accepting the job at City College, Bill was given space in the museum where he did much of his research for the next 35 years. The AMNH made Bill an Honorary Life Member and a Research Associate of the Museum. Following his retirement from City College in 1965, Bill worked at the AMNH for four years, before leaving New York to live at Penhaven.

Although Bill was trained in revisionary taxonomy and produced a number of important papers and monographs on pierids and crambids, his major contributions were his more popular writings. His books and photographs made entomology, especially lepidopterology, accessible and exciting to children and non-professionals as well as career biologists. Klots and his *Field Guide to the Eastern Butterflies* triggered my entomological Epiphany. My copy, which I sheepishly asked Bill to sign in 1988 was, of course, in miserable shape—its jacket long gone, the cover stained, spine broken, and pages riddled with penciled notes and highlighting. From the time it was first published in 1951, until Howe's (1975) *The Butterflies of North America* and the spate of butterfly books that followed, the field guide was the butterfly bible. It remains his most highly cited work.

Klots did much to popularize entomology through his photography. He was one of the early nature photographers to experiment with color and flash macrophotography. He was routinely sought out by publishers—his pictures peppered fillers in Sunday newspapers, magazines such as *Life* and *Family Circle*, encyclopedias, Audubon Society publications, and his own books as well as those of others. Unfortunately, much of his color photography was done using Ektachrome® slide films that tend to lose blues and yellows. His slide collection containing some 3000 slides was given to the Connecticut State Museum of Natural History. It contains a large number of topically grouped slides on metamorphosis, mimicry, crypsis, larval defenses, and other themes commonly seen in insects. Another special strength of the collection is the large number of determined larval Macrolepidoptera—a treasure, given the paucity of literature on immatures in this country.

The Field Guide explored much new ground in North American lepidopterology. It highlighted the relevance of ecological life zones to butterfly distributions. Bill was adept at identifying communities and particular plant associations that were likely to signal the presence of a butterfly species. He published several papers and presented numerous lectures on the zoogeography of arctic-alpine areas and bogs. In regard to the latter he wrote (1953:17) "No special environment will better repay the efforts of the butterfly collector." Bogs were a common denominator for three of his lifelong passions: *Boloria*, *Colias*, and crambids. The field guide was influential in drawing attention to the biological uniqueness of the New Jersey pine barrens.

Another area where Bill made important contributions is the study of genitalia for systematic characters. In particular, he advocated careful study of female structures. His treatment of Lepidoptera in Tuxen's (1956a) *Taxonomists' Glossary of Genitalia in Insects* has been his second most cited work.

Bill was exceptional among the North American lepidopterists in that he collected all families, from the most obscure and minute nepticulids to the more familiar groups like the Noctuoidea and Papilionoidea. Early in his career he published several faunal papers treating both Microlepidoptera and Macrolepidoptera. The majority of the specimens captured and pinned by Klots—the legacy of all collectors—are housed at the American Museum of Natural History. A small collection of 2100 butterflies and moths, mostly collected after 1975, went to the University of Connecticut. The taxonomic breadth of his collecting efforts is reflected in the numerous lepidopteran taxa that bear his name, which include members of eight families of butterflies and moths: *Acrolophus klotsi* Hasbrouck (Acrolophidae); *Gnorimoschema klotsi* Povolny (Gelechiidae); *Acleris klotsi* Obratsov and *Argyrotaenia klotsi* Obratsov (both Tortricidae); *Lycaena heteronea klotsi* (Field, 1936) (Lycaenidae); *Occidryas chalcidona klotsi* (dos Passos, 1938) (Nymphalidae); *Pyrausta klotsi* Munroe (Pyrilidae); *Ixala klotsi* Sperry (Geometridae); and *Drasteria klotsi* Richards and *Lasiestra klotsi* Richards (both Noctuidae). Klots patronyms in other insect orders attest to a broad influence Bill had on American entomology. These include the flea, *Jellisonia klotsi* Traub, which is also the type of its genus; the tephid wasp, *Pseudomethoca klotsi* Mickel; and the mosquito, *Aedes klotsi* Matheson.

Bill was an early and highly respected advocate for butterfly conservation in North America, arguing for habitat preservation as well as responsible collecting practices. Regarding the Schaus' Swallowtail (1951:174) he wrote "Now overcollecting by 'game hog' collectors has again reduced its numbers seriously in its last stand. NONE BUT MALES SHOULD BE COLLECTED, and then, at most, only one per collector. I believe most have enough sportsmanship to help protect the species and refuse to buy specimens at any price."

Both a charter and honorary life member of the Lepidopterists' Society, he was elected President in 1957 and Vice President in 1974. He also was President of the New York Entomological Society in 1940. From its inception, he served as a Counselor for the Xerces Society. Klots was a fellow of both the Royal Entomological Society and the Linnean Society of London and a member of the Explorers Club, Falconry Club of America, Society of American Naturalists, Society of Sigma Xi, Society of Systematic Zoology, Society of Taxonomists, and South London Entomological and Natural History Society. An authority on nomenclature, he attended two International Zoological Congresses (Co-



Life at Penhaven. Left: Bill in his bug room with his ever present bottle of Coca Cola®. No doubt, Bill spent more of his waking time in this tiny 60 square foot space off of the living room than in any other; right: Bill (circa 1980) dressed for some yard work . . . or perhaps for the baiting and collection of winter moths.

penhagen 1953 and London 1958) as a delegate to the Concilium on Zoological Nomenclature.

Beginning in 1970, Bill's health took a turn for the worse. He had hip operations in 1970 and 1972, neither of which was particularly successful—he was in discomfort for the rest of his life. Bill's penchant for tobacco caught up with him as well. His emphysema limited much of his activity later in life. I carry a vivid image of Bill disconnecting himself from his oxygen long enough to light up and take a few pulls on his pipe. Through the 1970's and early 1980's he continued with his entomological interests, but also read books on American history and mysteries, and attended Red Sox baseball games. Bill had a passion for literature on the American West, evidently his favorite was *The Journals of the Lewis and Clark Expedition*—it was a series Bill read and reread many times during his life.

His influence on me came in my teens, more than 20 years before I would meet him in person. When I finally met Bill, a little more than a year before his death, he was weakened by years of struggle with a bad hip and emphysema. Even then he was a giant to me. I think of him often, not as an old or frail man, but as a tireless collector, or in his words a "field man," slogging knee-deep through some bog, bagging lesser fritillaries and crambids.

I shall remember Bill for many things: in part for his proud and dignified demeanor; for his dry sense of humor, where puns were stacked on puns; for his colorfully eccentric attire that paired suits with moccasins or a favorite, old woolen army cap; but most of all for what he gave me as a young naturalist—knowledge and a passion for entomology—through his field guide, books, and photographs. More than any other North American biologist, his works have catalyzed and fueled the interests of legions of young entomologists. He will be sorely missed and long remembered.

PUBLICATIONS

Bill was a prolific writer as comfortable with revisionary taxonomy as with popular prose. It was his ability to pique interest in students of natural history that will be much of his legacy. Although professionally an entomologist, he published works on a variety of other subjects including arctic life, deserts, falconry, herpetology, mountaineering, wildflowers, and liverworts. His diverse entomological contributions appeared over a 60 year span and included taxonomic monographs, a field guide, several popular books, children's natural history sticker books, scientific and popular articles, text for encyclopedias, and dozens of book reviews. The list that follows was compiled from Bill's personal records and a curriculum vitae that he had prepared at the City College of New York. It is complete for Bill's books (first and English editions only) and Bill's major entomological contributions.

Bill authored 18 books; seven of which were co-written with Elsie, with Elsie as senior

author on three. Several of these were contract works for publishers looking for popular books during the heyday of color publishing, e.g., the series of nine sticker books published by Doubleday Press that were prepared under the aegis of the National Audubon Society; each included a set of color stickers that would be placed into appropriate spaces in the book to yield a splendidly illustrated natural history volume. The field guide was his most successful book with well over 120,000 copies being sold. *The World of Butterflies and Moths*, another popular work, appeared in seven different languages.

The following list may be lacking in its coverage of popular articles and does not include his book reviews and contributions to encyclopedias. Bill frequently was called upon for book reviews; as many as twenty five appeared in *Natural History Magazine* and the *Quarterly Review of Biology* by the year 1959. The breadth of his expertise as a natural historian is reflected by the subject matter of his reviews—besides Lepidoptera, Bill reviewed books on other insect groups, falconry, hiking and mountaineering, and vertebrate wildlife. Most of his entomological reviews appeared in the *Bulletin of the Entomological Society of America*, *Journal of the New York Entomological Society*, and the *Quarterly Review of Biology*. His abilities as a writer made him popular with encyclopedia publishers; Bill's treatments of insects appeared in *Compton's Encyclopedia*, *Encyclopedia Britannica*, *Encyclopedia of Earth Sciences*, *Grolier Society's Book of Knowledge*, and *World Book*. In the 1956 and 1957 edition of the latter, Klots also contributed a treatment on Falconry.

Books

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- 1960 Tropical butterflies. Children's Press, Chicago. 160 pp.
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- 1929b A revision of the genus *Eurema* Hübner (Lepidoptera, Pieridae). Part II, New World species, taxonomy and synonymy. Entomol. Am. 9:99-171.
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- 1930a Notes on Amphibia and Lacertilia collected at Weymouth, New Jersey. Copeia 173:107-111.
- 1930b A new subspecies of *Ascia monuste* (L.) from Lower California (Lepidoptera, Pieridae). Pan-Pacif. Entomol. 6:145-147.
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- 1930d Diurnal Lepidoptera from Wyoming and Colorado. Bull. Brooklyn Entomol. Soc. 25:147-170.
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- 1933b Directions for collecting and preserving insects. Wards Natural Science Establishment, Rochester, New York. 30 pp. [with two later editions].
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- 1935b A new *Colias* from South Dakota (Lepidoptera: Pieridae). Amer. Mus. Novitates No. 767. 2 pp.
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- 1945a Experiments on DDT residual spray treatment of C-47 aircraft. 1st Troop Carrier Command, U.S. Army Air Force. 33 pp.
- 1945b Preliminary report on disinsectization of aircraft, using DDT. Rep. Army Air Force Center, Orlando, Florida. 30 pp.
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- 1966c The larva of *Amblyscirtes samoset* (Scudder) (Lepidoptera, Hesperidae). *J. New York Entomol. Soc.* 74:185-188.
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CHARLES GORDON CAMPBELL DICKSON

Charles Dickson was born on 9 December 1907 at Gardens in Cape Town and died in that city on 30 August 1991. He was probably the foremost South African lepidopterist of this century, discovering no fewer than 38 new lepidopteran species (13 named after him) in the mountains and hills of the Western Cape. Through patient fieldwork and life-history research, he revised some genera and described an amazing 102 new butterfly species and subspecies (including 7 in the forthcoming second edition of Pennington's *Butterflies of Southern Africa*)—approximately 10% of the total fauna in the subregion. Only the great pioneer taxonomist Roland Trimen exceeded this output for South African butterflies.

Charles became interested in butterflies at an early age, partly through his family's friendship with Roland Trimen. In the early days he also was influenced by Dr. Hesse and Dr. Skaife, and his interest was coupled with moths, which he subsequently collected for the Transvaal Museum.

Butterflies, however, were always closest to his heart, and Charles became the foremost authority on the butterflies of the Cape. In the 1930's he met Gowan C. Clark, who was South Africa's foremost butterfly illustrator, and for more than a quarter of a century he collected life-history material for Clark. This collaboration produced the 1971 book *Life Histories of the South African Lycaenid Butterflies*. Charles wrote and compiled it, making use of Gowan Clark's illustrations and notes, which he supplemented with his own. Clark, who had passed away some years previously, was acknowledged as the senior author—a gesture of typical modesty on the part of Charles Dickson. The value of this work was immediately apparent and gained for him an honorary M.Sc. from the University of Cape Town.

Charles was particularly interested in the myrmecophilous Lycaenidae of South Africa, in which the Western Cape is particularly rich. Together with his good friend Dr. Andre Claassens, he pioneered local research on this fascinating aspect of butterfly life. His work with Claassens culminated in the 1980 book *Butterflies of the Table Mountain Range*, which dealt exclusively with the butterfly species of the Cape Peninsula.

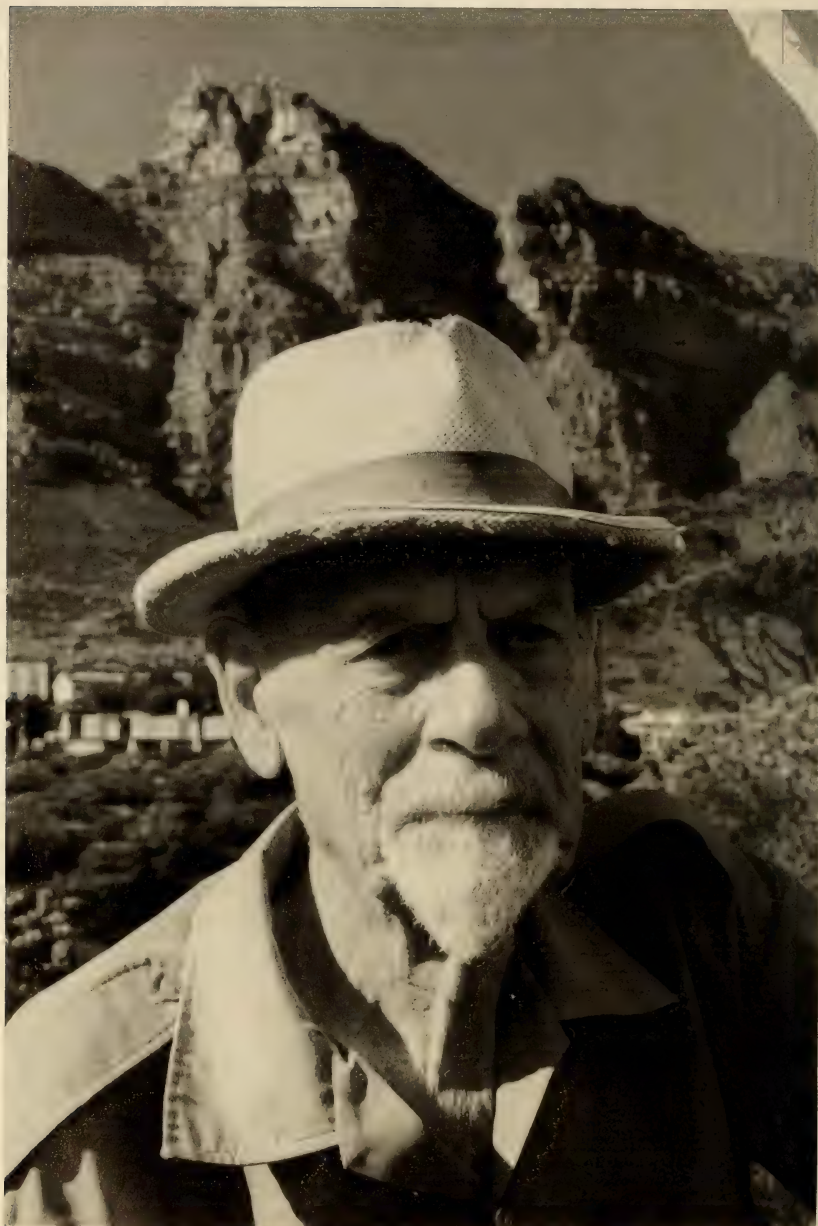
When K. M. Pennington died in 1974, leaving a skeleton manuscript dealing with the butterflies of the Southern African subregion, Charles was asked to complete the book. This he did with characteristic zeal, and *Pennington's Butterflies of Southern Africa* was published in 1978. This book remains the definitive work on the butterflies of this subregion. At the time of his death, Charles was putting the finishing touches on the revised second edition of *Pennington's Butterflies*, which should be published in 1992.

Apart from butterflies, Charles's other great passion was vintage motor cars of old British and Continental marques, and steam locomotives. He was also a fierce advocate of retaining the early Cape place names.

Charles was a wonderful correspondent with numerous local and international lepidopterists. He corresponded with my father, Bill Henning, for 30 years, often exchanging letters with him every week. Unfortunately, eye problems late in life curtailed his prolific output of letters. Charles was a familiar figure in Cape Town, driving his vintage Riley. In fact, my first view of Charles Dickson was behind the wheel of the Riley when he came to pick me up outside the University of Cape Town in the 1970's. He was a particularly kind and generous person, and his many kindnesses to my father, brother, and myself will never be forgotten. His encouragement started me on my writing career, and he proof-read my early attempts at scientific writing. I will always remember him with affection as my mentor and friend.

ALPHABETICAL LIST OF TAXA DESCRIBED BY CHARLES DICKSON

Aloeides apicalis (1968), *Aloeides arida* (1968), *Aloeides bamptoni* (1977), *Aloeides braueri* (1968), *Aloeides caledoni* (1973), *Aloeides carolynnae* (1983), *Aloeides clarki* (1968), *Aloeides damarensis mashona* (1973), *Aloeides depicta* (1968), *Aloeides dryas* (1968), *Aloeides gowani* (1968), *Aloeides henningi* (1968), *Aloeides juana* (1968), *Aloeides kaplani* (1977), *Aloeides lutescens* (1965), *Aloeides macmasteri* (1973), *Aloeides*



margaretae (1968), *Aloeides molomo coalescens* (1973), *Aloeides molomo krooni* (1973), *Aloeides natalensis* (1968), *Aloeides nollothi* (1977), *Aloeides oreas* (1968), *Aloeides pallida grandis* (1968), *Aloeides pallida littoralis* (1968), *Aloeides penningtoni* (1968), *Aloeides plowesi* (1973), *Aloeides pringlei* (1976), *Aloeides quickelbergae* (1968), *Aloeides*

rileyi (1976), *Aloeides stevensoni* (1973), *Aloeides susanae* (1973), *Aloeides swanepoeli* (1973), *Aloeides trimeni southeyae* (1973), *Aloeides trimeni trimeni* (1973), *Aloeides vansonii* (1968).

Argyrocupha malagrida cedrusmontana (1975), *Argyrocupha malagrida maryae* (1980), *Argyrocupha malagrida paarlensis* (1967).

Chrysoritis cottrelli (1975).

Crudaria wykehami (1983).

Gonatomyrina henningi (1976).

Iolaus (*Epamera*) *mimosae pamela* (1976).

Lepidochrysops balli (1985), *Lepidochrysops braueri* (1966), *Lepidochrysops jamesi claassensi* (1982), *Lepidochrysops oreas junae* (1974), *Lepidochrysops penningtoni* (1969), *Lepidochrysops pringlei* (1982), *Lepidochrysops southeyi* (1967), *Lepidochrysops titei* (1976).

Lycaena clarki (1971).

Myrina silenus penningtoni (1971).

Phasis braueri (1968), *Phasis thero cedarbergae* (1974).

Poecilmitis atlantica (1966), *Poecilmitis balli* (1980), *Poecilmitis bamptoni* (1976), *Poecilmitis beaufortia beaufortia* (1966), *Poecilmitis beaufortia charlesi* (1970), *Poecilmitis brooksi tearei* (1966), *Poecilmitis daphne* (1975), *Poecilmitis felthami dukei* (1967), *Poecilmitis hyperion* (1975), *Poecilmitis lysander hantamsbergae* (1978), *Poecilmitis nigricans zwartbergae* (1982), *Poecilmitis palmus margueritae* (1982), *Poecilmitis pyr-oeis hersaleki* (1970), *Poecilmitis rileyi* (1966), *Poecilmitis stepheni* (1978), *Poecilmitis swanepoeli* (1965), *Poecilmitis turneri amatola* (1967), *Poecilmitis violescens* (1971), *Poecilmitis wykehami* (1980).

Pseudonympha camdeboo (1981), *Pseudonympha southeyi kamiesbergensis* (1967), *Pseudonympha southeyi wykehami* (1967), *Pseudonympha trimenii nieuweveldensis* (1966), *Pseudonympha trimenii ruthae* (1966).

Stugeta bowkeri henningi (1980), *Stugeta bowkeri tearei* (1980).

Tarsocera southyae (1969).

Thestor basutus capeneri (1972), *Thestor kaplani* (1971), *Thestor pringlei* (1976), *Thestor rossouwii* (1971).

Torynesis hawequas (1973), *Torynesis mintha picquetbergensis* (1967), *Torynesis pringlei* (1979).

Trimenia argyroplaga (1967), *Trimenia macmasteri macmasteri* (1968), *Trimenia macmasteri mijiburghi* (1980), *Trimenia wykehami* (1969).

Tsitana tulbagha kaplani (1976).

Tylopaedia sardonix peringueyi (1969).

Zintha hintza krooni (1973).

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1943

2. The life-history of *Phasis chrysaor* (Trim.) (Lepidoptera: Lycaenidae). J. Entomol. Soc. S. Afr. 6:37-47.

1944

3. The life-history of *Cupido thespis* L. (Lepidoptera: Lycaenidae). J. Entomol. Soc. S. Afr. 7:20-29.

4. Recently observed food-plants of some Cape lepidopterous larvae. J. Entomol. Soc. S. Afr. 7:96-99.

1945

5. Recently observed food-plants of some Cape lepidopterous larvae (2nd series). J. Entomol. Soc. S. Afr. 8:150-153.
6. The life history of *Phasis palmus* Cram. (Lepidoptera: Lycaenidae). J. Entomol. Soc. S. Afr. 8:99-110.

1947

7. The life history of *Phasis thysbe* L. var. *nigricans* Aur. (Lepidoptera: Lycaenidae). J. Entomol. Soc. S. Afr. 9:178-192.
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9. Recently observed food-plants of some Cape lepidopterous larvae (3rd series). J. Entomol. S. Afr. 9:127-130.

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10. The life history of *Phasis pyroetis* Trim. (Lepidoptera: Lycaenidae). J. Entomol. Soc. S. Afr. 11:50-62.

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1954

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19. Clark, G. C. & C. G. C. Dickson. The life-history of *Precis octavia* (Cram.) (Lepidoptera: Nymphalidae). J. Entomol. Soc. S. Afr. 20:257-259.
20. Clark, G. C. & C. G. C. Dickson. On the life-history of *Leptomyrina lara* (L.) and the reclassification of the Natal form, *gorgias* (Stoll) (Lepidoptera: Lycaenidae). J. Entomol. Soc. S. Afr. 20:333-334.
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1959

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1962

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26. Clarke, C. A., C. G. C. Dickson & P. M. Sheppard. Larval colour pattern in *Papilio demodocus*. Evolution 17:130-137.

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28. Obituary—Gowan G. G. Clark. Entomol. Rec. J. Var. 76:173-174.

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33. The life history of *Xanthopan morgani* (Wlk.) (Lepidoptera: Sphingidae). J. Entomol. Soc. S. Afr. 28:230-232.
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1966

35. A new subspecies of *Pseudonympha trimenii* Butler (Lepidoptera: Satyridae) from the Eastern Cape Province. Entomol. Rec. J. Var. 78:85-87.
36. A new species of *Poecilmitis* Butler (Lepidoptera: Lycaenidae) from the Great Karroo. Entomol. Rec. J. Var. 78:109-110.
37. A Cape Coastal *Poecilmitis* Butler (Lepidoptera: Lycaenidae) previously unknown. Entomol. Rec. J. Var. 78:181-182.
38. A new species of *Lepidochrysops* Hedicke (Lepidoptera: Lycaenidae) from the Western Cape Province. Entomol. Rec. J. Var. 78:189-192.
39. Revisional notes on the Cape lycaenid *Poecilmitis brooksi* Riley, with the description of a recently-recognised race of this species. Entomol. Rec. J. Var. 78:217-219.
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43. A new subspecies of the Cape lycaenid *Poecilmitis felthami* (Trimen) (Lepidoptera: Lycaenidae). Entomol. Rec. J. Var. 79:65-66.
44. Two new subspecies of *Pseudonympha southei* (Pennington) from the Western Cape Province. Entomol. Rec. J. Var. 79:93-97.
45. Observations on the Cape lycaenid *Phasis malagrida* (Wallengren), with the description of a new race. Entomol. Rec. J. Var. 79:123-125.
46. Notes on the Cape satyrid butterfly *Torynesis mintha* (Geyer) with a description of a new race. Entomol. Rec. J. Var. 79:160-162.
47. Some observations on *Poecilmitis turneri* Riley (Lepidoptera: Lycaenidae). Entomol. Rec. J. Var. 79:209-211.
48. Some comments on the *Phasis wallengrenii* (Trimen) group (Lepidoptera: Lycaenidae) with a description of a new species. Entomol. Rec. J. Var. 79:267-270.
49. Dickson, C. G. C. & J. C. McMaster. Some observations on *Poecilmitis turneri* Riley (Lepidoptera: Lycaenidae), with a description of a new race. Entomol. Rec. J. Var. 79:209-211.

1968

50. A further new species of the *Phasis wallengrenii* (Trimen) complex (Lepidoptera: Lycaenidae). Entomol. Rec. J. Var. 80:89-92.
51. Some observations on the *Phasis thero* (L.) group (Lepidoptera: Lycaenidae) with a description of a new species. Entomol. Rec. J. Var. 80:267-270.
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55. Descriptions of the neallotypes of two Cape *Poecilmitis* Butler (Lepidoptera: Lycaenidae). Entomol. Rec. J. Var. 81:185-187.
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57. On the status of *Phasis sardonix* ab. *peringueyi* Aurivillius (Lepidoptera: Lycaenidae), and the selection of a neallotype female. Entomol. Rec. J. Var. 81:313-315.

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59. A new race of *Poecilmitis pyroëis* Trimen (Lepidoptera: Lycaenidae) from the Eastern Cape Province. Entomol. Rec. J. Var. 82:157-159.

1971

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61. A further new member of the *Poecilmitis thysbe* (L.) group (Lepidoptera: Lycaenidae) from the Roggeveld Mountains. Entomol. Rec. J. Var. 83:1-2.
62. A further new species of *Thestor* Hubner (Lepidoptera: Lycaenidae) from the Western Cape. Entomol. Rec. J. Var. 83:155-159.
63. Dickson, C. G. C. & R. D. Stephen. A new western cape species of *Thestor* Hubner (Lepidoptera: Lycaenidae). Entomol. Rec. J. Var. 83:131-135.
64. Dickson, C. G. C. & R. D. Stephen. A new race of *Myrina silenus* (F.) (Lepidoptera: Lycaenidae) from the North Western Cape. Entomol. Rec. J. Var. 83:255-259.

1972

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1973

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69. Tite, G. E. & C. G. C. Dickson. The genus *Aloeides* and allied genera (Lepidoptera: Lycaenidae). Bull. Brit. Mus. Nat. Hist. (Entomol.) 29:225-280.

1974

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76. Dickson, C. G. C. & R. D. Stephen. An additional new race of *Argyrocupha malagrida* (Wallengren) (Lepidoptera: Lycaenidae). Entomol. Rec. J. Var. 87:129-132.

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1980

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90. Dickson, C. G. C. & W. H. Henning. A new race of *Argyrocupha malagrida* (Wallengren) (Lepidoptera: Lycaenidae) from the Western Cape Province. Entomol. Rec. J. Var. 92:297-300.

1981-1982

- 91-93. Four new South African butterflies. Entomol. Rec. J. Var. 93:219-221; 94:32-35, 41-44.

1982-1983

- 94-95. Three new lycaenid butterflies from the South Western Cape Province. Entomol. Rec. J. Var. 94:222-224; 95:1-6.

1985

96. A new *Lepidochrysops* Hedicke (Lepidoptera: Lycaenidae) from the South Western Cape Province. Entomol. Rec. J. Var. 97:1-5.

1986

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1991

99. Descriptions of the penultimate and final instar larvae of *Durbania saga* Trimen (Lepidoptera: Lycaenidae). Metamorphosis 2(3):27-28.

STEPHEN FRANK HENNING, 5 *Alexandra Street, Florida 1709, South Africa.*

FEATURE PHOTOGRAPH

ATTRACTING AND PHOTOGRAPHING *AGRIAS AMYDON* (NYMPHALIDAE) IN BRAZIL

I have visited the tropics 19 times within the last 22 years; 15 of those trips have been to Central and South America where numerous species of *Agrias* occur. Yet I had neither collected nor photographed a single individual of *Agrias* until my most recent visit to Rondonia, Brazil, in 1992.

As with many tropical nymphalids, *Agrias* are attracted to organic substances, such as fermenting fruit, decaying fish, feces, and urine. *Agrias claudina* and *Agrias amydon philatelica* previously have been photographed feeding upon fermenting fruit (by J. Nation and P. DeVries). There is anecdotal evidence that *Agrias* are attracted to large decaying animals (e.g., cows) as well.

During three trips to Fazenda Rancho Grande near Cacaullandia, about 60 km south of Ariquemes, Rondonia, Brazil, I concentrated on photographing butterflies. To attract my subjects, I used fermenting fruit (banana and papaya), feces, feces mixed with urine, fresh urine, urine several days old, freshwater fish (usually 2-3 pounds) in various stages of decomposition, and rotting sardines. These baits attracted numerous nymphalids, including *Caligo*, *Morpho*, *Adelpha*, *Doxocopa*, *Batesia*, *Napeocles*, and *Prepona*, but no *Agrias*.

During my last trip to Rondonia, five or six participants collected individuals of *Agrias amydon*. One was taken in flight, one was picked by hand from beneath a leaf, one was attracted to urine on the ground, and several were caught in butterfly traps baited with rotting fish. On 23 April 1992, I photographed a fresh male of *Agrias amydon bellatrix* (see Plate 1) on a wet dirt road through virgin forest about 15-20 km east of Fazenda Rancho Grande. The individual was attracted by urine and white toilet paper wetted with 2-3 week old liquefied fish. The butterfly approached the bait, flying slowly in circles. After landing on the ground it changed positions, sipping various fluids, most of the time with its wings held closed over the thorax. On several occasions it took off and returned a short time later.

I photographed the individual using a Nikon FA camera fitted with a Micro-NIKKOR 200 mm 1:4 lens. A Nikon SB-15 electronic flash attached to the hot shoe on the camera was used in conjunction with Ektachrome 200 ASA slide film. The Nikon FA camera has a TTL (through the lens) metering system that automatically admits the necessary amount of light from the Nikon SB-15 flash when in TTL mode. Exposures were taken at 1/250 sec at aperture f-32. Specific determination of the butterfly was confirmed by Thomas Emmel.

GEORGE O. KRIZEK, 2111 Bancroft Place, N.W., Washington, D.C. 20008.



Plate 1. *Agrias amydon bellatrix*.

INDEX TO VOLUME 46

(New names in **Boldface**)

- aberration, 238
acis gossei, Strymon, 124
 Ackery, P. R., 273
Acronicta
 fragilis, 221
 heitzmani, 220
Acronictinae, 220
 Adams, James K., 160
Aegicerus corniculatus, 174
Aethiopana honorius, 210
A Field Guide to Eastern Butterflies (book review), 307
 Africa, 54
agamemnon, *Graphium*, 86
Aglais urticae, 302
Agraulis vanillae insularis, 120
Agrias amydon, 334
albaniana, *Choristoneura*, 269
Aleuron, 73
almana javana, *Precis*, 87
ammon erembis, *Cyclargus*, 124
 Anak Krakatau, 83
Anartia jatrophae jamaicensis, 124
andraemon, *Heracles*, 125
Anetia jaegeri, 273
angellus, *Halotus*, 184
Anthene emolus, 88
anomala, *Hypolimnas*, 88
Antheraea mylitta, 106
 ants, 203
 aorta, 215
apelles, *Hypochrysops*, 174
aphractoia, *Paratrytone*, 21
Appias drusilla poeyi, 124
aratus, *Jamides*, 88
A Revision of the Indo-Australian Genus Attacus (book review), 166, 167
 Archbold Biological Station, 138
 arctic butterfly, 110
Arctiidae, 160
arge, *Pyrrhogyra neaerea*, 77
argentea, *Paratrytone*, 21
Arhopala pseudocentaurus, 88
aristolochiae, *Pachliopta*, 86
 Arizona, 159
arthemis, *Limenitis*, 216
Arthromastix
 lauralis, 75
 verecundalis (new combination), 75
Ascia monuste eubotea, 124
aspidos, *Larinopoda*, 208
astarte astarte, *Catacore*, 77
Asteraceae, 195
atala, *Eumaeus*, 124
atlites, *Precis*, 87
 attraction (to pheromones), 265
augias, *Telicota*, 89
aurorina, *Cithaerias*, 44
 Austin, George T., 240
 Australia, 24, 173, 195
Avicennia marina, 174
azin, *Poanes*, 17, 21
badiana, *Bebearia*, 66
badiana dealbata, *Bebearia*, 66
badiana taveta, *Bebearia*, 66
Baccharis halimifolia, 195
 Bailey, Audette J. A., 233
balanotes, *Oidaematophorus*, 195
barroni, *Paratrytone*, 21
bataviana, *Danaus chrysippus*, 87
batesi, *Ochlodes*, 21
Bebearia
 badiana, 66
 badiana dealbata, 66
 badiana taveta, 66
 cocalia (= *mardania*, new syn.), 57
 continentalis (= *katera*, new syn.), 60
 guineensis, 63
 insularis Schultze (= *katera*, new syn.), 60
 mardania, 57
 mardania cocalioides, 59
 orientis, 64
 orientis insularis Kielland, 64
 paludicola (= *guineensis*, new syn.), 63
 senegalensis, 59
 senegalensis katera, 60
 theognis, 61
 behavior, 24, 77, 110
benito (ex *Poanes*), 3
bilinealis, *Oligostigma* (= *Microdracon* = *Parapoynx*), 76
 biogeography, 235, 275
Biologia y Morfologia de las Orugas: Lepidoptera, Vol. 6: Syssphingidae, Saturniidae, Endromidae, Lasiocampidae, Drepanidae, Thyatiridae, Notodontidae, Hypsidae (book review), 246
 biological control, 195
 biology, 195, 203, 233
bitje, *Pentila*, 206
blanda, *Eurema*, 87
 blood flow, 215
bochus, *Jamides*, 88
boeticus, *Lampides*, 88
bolina, *Hypolimnas*, 24

- Bombyx mori*, 106
Borbo cinnara, 88
 Brazil, 77, 255
 Brower, Lincoln P., 97
Buggy Books: A Guide to Juvenile and Popular Books on Insects and Their Relatives (book review), 164
 Burns, John M., 1, 182

 Calhoun, John, 238
californiella, *Coenochroa*, 43
 Callaghan, Curtis J., 203
 Calvert, William H., 97
 cambium miner, 70
canadensis, *Synanthedon*, 265
capta, *Poanes*, 19, 21
captiosa, *Disphragis*, 159
 cardiac output, 215
cardui, *Vanessa*, 235
 Caribbean biogeography, 119
Carmentis
 flaschkai, 265
 verecunda, 265
carnuta, *Ptelina*, 204
cassius theonus, *Leptotes*, 124
Catacore
 astarte astarte, 77
 kolyma connectens, 77
Catocala
 judith, 216
 sappho, 161
 ulalume, 161
Catochrysops strabo, 88
Catopsilia pomona, 87
 Cayman Brac, 119
Ceratoclasia verecundalis, 76
 Cayman Islands, 119
celeno, *Jamides*, 88
Ceriodops tagal, 174
charitonia ramsdeni, *Heliconius*, 122
 check list, 280
 checklist placement, 159
 Chihuahua, 128
 Chile, 39
chilensis, *Coenochroa*, 39
Choristoneura
 albaniana, 269
 lapponana, 269
chrysippus bataviana, *Danaus*, 87
cinnara, *Borbo*, 88
Cithaerias
 aurorina, 44
 menander, 50
 pyritosa, 50
Citrinophila
 erastus, 208
 marginalis, 207
 clarus, *Epargyreus*, 216
 Clayton, Dale L., 110
 clearwing moth, 265
cleobaea, *Lycorea*, 275
cleophile, *Danaus*, 274
 cloud-response, 97
clymena, *Diaethria*, 77
cnejus, *Euchrysops*, 88
cocalia, *Bebearia* (= *mardania*, new syn.), 57
cocalioides, *Bebearia mardania*, 59
Coenochroa
 californiella, 43
 chilensis, 39
 dentata, 43
 illibella, 42
Coenodomus, 280
Cola nitida, 203
 cola forest, 203
 Colombia, 44
 color patterns, 77
Coloradia prchali, 128
 Colorado, 110
 coloration, 24
 common eggfly, 24
 community structure, 255
connectens, *Catacore kolyma*, 77
confucius, *Potanthus*, 88
conjunctus, *Pelopidas*, 88
 conservation, 83
 Constantino, Luis M., 44
continentalis, *Bebearia* (= *katera*, new syn.), 60
core, *Euploea*, 30
cornesi, *Eresimera*, 207
corniculatum, *Aegicerus*, 174
 couplet, 265
 Covell, Charles V., Jr., 220
 Crambidae, 159
Crematogaster, 210
cresphontes ab. "maxwelli", *Papilio*, 238
chiron, *Marpesia*, 77
chromalis, *Nothomastix*, 75
 Cuba, 273
 Cucullinae, 220
Cyclargus ammon erembi, 124
cydaria, *Pentila picena*, 206
Cymaenes tripunctus, 226

daira palmira, *Eurema*, 124
Danainae, 97, 120, 273
Danaus
 chrysippus bataviana, 87
 cleophile, 273
 genutia, 87
 melanippus, 88
 plexippus, 97, 120

- Dang, P. T., 269
danielana, *Memphis echemus*, 124
 Dash, M. C., 106
 Davis, Donald R., 240
dealbata, *Bebearia badiana*, 66
 de Araujo, Aldo Mellener, 255
decepta, *Paratrytone*, 21
decostalis, *Heleithia*, 159
 defensive behavior, 203
dentata, *Coenochroa*, 43
Diaethria clymena, 77
 Dickson, Charles Gordon Campbell (obituary), 325
Die Raupen der Schmetterlinge Europas (book review), 166
dioica, *Urtica*, 303
Discover Butterflies! An Activity Book for Families, Students, and Teachers (book review), 244
 dispersal, 235
Disphragis captiosa, 159
 distribution, 128, 134, 138, 159, 226, 230, 269, 273, 298, 301
Distribution of Butterflies in New Mexico (Lepidoptera: Hesperioidea and Papilionioidea) (book review), 241
diversa, *Tetrarhanis*, 209
 diversity, 255, 298, 301
domingo, *Urbanus proteus*, 125
 Dopler crystal system, 215
 dorsal vessel, 215
 Drummond, Boyce A., 164
drusilla poeyi, *Appias*, 124
Dryas iulia zoe, 119
Dulcedo, 44
 dung mimicry, 70
dunia, *Epitola*, 209
 early stages, 70, 161
echemus danielana, *Memphis*, 124
 Ecuador, 73
ecuadora, *Haetera piera*, 50
 eggs, 73, 233
 Eichlin, Thomas D., 243, 265
elathea, *Eurema*, 124
electra, *Hemileuca*, cover illustration issue 2
 Emmel, Thomas C., 244
emolus, *Anthene*, 88
 Encyrtidae, 233
 endangered, 233
Epargyreus clarus, 216
epicurus, *Hypochrysops*, 174
Epipaschia, 280
 Epipaschiinae, 280
 epiphyll feeding, 203
Epitola dunia, 209
erastus, *Citrinophila*, 208
erembis, *Cyclargus ammon*, 124
Eresiomera cornesi, 207
erylus, *Hypolyceana*, 88
eubotea, *Ascia monuste*, 124
Euchrysops cnejus, 88
 Eulophidae, 233
Eumaeus atala, 124
Euploea
 core, 30
 modesta, 87
Euptoieta hegesia, 122
 Eurasian, 302
Eurema
 blanda, 87
 daira palmira, 124
 elathea, 124
 hecabe, 87
 lisa euterpe, 124
 nicippe, 124
 nise, 124
euterpe, *Eurema lisa*, 124
evarete zonalis, *Junonia*, 122
 Fabrician species, 54
 faunal development, 83
 faunal survey, 83, 138, 220
ferruginea, *Hirundinia*, 77
filenus, *Hemiargus hanno*, 124
flaschkai, *Carmenta*, 265
 flight pattern, 110
 flight period, 173
 Florida, 138, 195, 238
 food plant, 27, 70, 138, 161, 174, 195
 foraging behavior, 77
fragilis, *Acronicta*, 221
 Gall, Lawrence F., 242
 Garraway, Eric, 233
 generic group, 182
 genitalia (male and female), 1, 39, 42, 45, 48, 54, 67, 128, 182, 220, 265
genoveva, *Junonia*, 122
genutia, *Danaus*, 87
 Glassberg, Jeffrey, 302
glenni, *Oidaematophorus*, 197
 Gonzalez, Jose Valentin Herrera (obituary), 248
 gooseberry, 70
gossei, *Strymon acis*, 124
 Grand Cayman, 119
grandis, *Oidaematophorus*, 197
Graphium
 agamemnon, 86
 sarpedon, 86
 Grossulariaceae, 70

- guineensis*, *Bebearia*, 63
guttatus, *Parnara*, 89
- habitat, 128
 habitat preference, 110
- Haetera*
macleannania, 44, 50
piera piera, 50
piera ecuadora, 50
- Haeterini, 44
halimifolia, *Baccharis*, 195
- Halotus*
angellus, 184
jonaveriorum, 186
rica, 188
- Hancock, David L., 54
hanno filenus, *Hemiargus*, 124
- Haseler, W. H., 195
Hasora taminatus, 89
- heart function, 215
- hecabe*, *Eurema*, 87
hegesia, *Euptoieta*, 122
- heitmani*, *Acronicta*, 220
- Heleithia decostalis*, 159
- helena*, *Troides*, 87
- Heliconius charitonia ramsdeni*, 122
- Hemiargus hanno filenus*, 124
- Hemileuca electra*, cover illustration is-
 sue 2
- Hemileucinae, 128
- Henning, Stephen Frank, 325
- Heppner, John B., 301
- Heracles andraemon*, 125
- Herrera G., Jose Valentin (obituary), 248
- Hesperiidae, 1, 88, 125, 141, 182
- Hidalgo County, 160
- Highlands County, Florida, 138
- Hill, C. J., 173
- hilltopping, 110
- Hirundinia ferruginea*, 77
- Hispaniola, 273
- hobomok*, *Poanes*, 3, 21
- Holarctic, 269
- holotype, 1, 39, 220, 238, 265
- homerus*, *Papilio*, 233
- honorius*, *Aethiopana*, 210
- host plant, 138, 195
- hurtellum*, *Ribes*, 70
- hylas*, *Neptis*, 87
- hylax*, *Zizula*, 88
- Hylephila phyleus*, 126
- Hyles lineata*, cover issue 4
- hypoasia*, *Pseudohaetera*, 44, 50
- Hypochrysops*
apelles, 174
epicurus, 174
- Hypolimnas*
anomala, 88
bolina, 24
missippus, 35
Hypolyceana erylus, 88
- Ideopsis juvena*, 87
- illibella*, *Coenochroa*, 42
- Indian tasar silkworm, 106
- Indonesia, 83
- inimica*, *Poanes*, 20, 21
- insect diversity, 255
- insularis*, *Agraulis vanillae*, 120
- insularis* Schultze, *Bebearia* (= *katera*, new
 syn.), 60
- insularis* Kielland, *Bebearia orientis*, 64
- intrasexual competition, 24
- introduction, 302
- island biogeography, 83, 119, 000
- ulia zoe*, *Dryas* 119
- jaegeri*, *Anetia*, 273
- Jamaica, 233, 273
- jamaicensis*, *Anartia jatrophae*, 124
- Jamides*
aratus, 88
bochus, 88
celeno, 88
- janardana*, *Mycalesis*, 87
- Janzen, Daniel H., 167
- jatrophae jamaicensis*, *Anartia*, 124
- javana*, *Precis almana*, 87
- joannis*, *Lithohane*, 220
- jonaveriorum*, *Halotus*, 186
- judith*, *Catocala*, 216
- Junonia*
evarete zonalis, 122
genoveva, 122
- juvena*, *Ideopsis*, 87
- katera*, *Bebearia senegalensis*, 60
- kellicotti*, *Oidaematophorus*, 197
- kershawii*, *Vanessa*, 235
- kirbyi*, *Ornipholidotos*, 207
- Klots, Alexander Barrett (obituary), 314
- klotsi*, *Nothomastix* (new combination), 76
- kolyma connectens*, *Catacore*, 77
- Krizek, George O., 334
- Lacinipolia*
rodora, 79
vicina, 80
- lacteodactylus*, *Oidaematophorus*, 197
- Lake Wales Ridge, 138
- Lampides boeticus*, 88
- laothoe*, *Temenis*, 77
- lapponana*, 269
- Larinopoda aspidos*, 208

- larvae, 70, 161, 197
Larvae of Owlet Moths (Noctuidae) (book review), 243
 larval behavior, 70, 203
lauralis, *Salbia*, 76
 Lawton, Robert O., 97
 lectotype designations, 54
leda, *Melanitis*, 87
 Lemaire, Claude, 128
Leptotes cassius theonus, 124
 Leuschner, Ron, 79, 159
libentina, *Mimeresia*, 207
 lichen moth, 160
 life history, 161, 197, 233
Limenitis arthemis, 216
lineata, *Hyles*, cover issue 4
Liptena
 opaca, 208
 similis, 208
 Lipteninae, 203
lisa euterpe, *Eurema*, 124
Lista, 280
Lithophane joannis, 220
 Lithosiinae, 160
Locastra, 280
lubricans, *Polytremis*, 88
lupulina, *Poanes*, 20, 21
 Lycaenidae, 88, 124, 173, 203
Lycomorphodes sordida, 160
Lycorea cleobaea, 275
lysizone, *Zizina otis*, 88

Macalla, 280
 Mack, Callie, cover illustrations, issues 1, 2, 3 & 4
macleaniania, *Haetera*, 50
 MacNeill, C. Don, 248
macneilli, *Poanes*, 17, 21
 mangrove, 173
 man-made habitats, 255
mardania, *Bebearia*, 57
mardania cocalioides, *Bebearia*, 59
marginalis, *Citrinophila*, 207
marina, *Avicennia*, 174
Marpesia
 chiron, 77
 norica, 77
maritalis, *Strymon*, 124
 Martins, M., 77
 mate-locating behavior, 24
 mate-searching, 110
 Mather, Bryant, 159
 "maxwelli" (ab.), *Papilio crespontes*, 238
medus, *Orsotriaena*, 87
melane, *Poanes*, 12, 21
melanocholicus, *Tyrannus*, 77
melanippus, *Danaus*, 88

Melanitis leda, 87
melinus, *Strymon*, cover issue 1
memnon, *Papilio*, 86
Memphis echemus danielana, 124
menander, *Cithaerias*, 50
 Metzler, Eric H., 220
 Mexico, 79, 97, 128, 159
 microclimate, 97
Microdracon, 76
 migration, 235
Miletus symethus, 88
 Miller, Jacqueline Y., 73
 Miller, Lee D., 119
Mimeresia libentina, 207
 mimicry, 160
 Minno, Marc C., 138
 Mishra, C. S. K., 106
missippus, *Hypolimnas*, 35
modesta, *Euploea*, 87
 monarch, 97
monticola, *Poanes*, 19, 21
monuste eubotea, *Ascia*, 124
Moths of Australia (book review), 311, 313
 Munroe, Eugene, 75, 159
Mycalasis janardana, 87

 national record, 79, 159
 Nayak, B. K., 106
neaerea arge, *Pyrrhogyra*, 77
 Nearctic, 1
 nectar, 173
 nectar source, 138
 Neotropical, 1, 44, 73, 160, 182, 298, 301
 Neotropics, 39
Neptis hylas, 87
 New, T. R., 83
 new records, 119, 159, 160, 302
 New York, 302
nicippe, *Eurema*, 124
Niconiades, 182
 Nigeria, 203
nigeriana, *Pentila*, 204
nise, *Eurema*, 124
nitida, *Cola*, 203
niveolimbus, *Poanes*, 19, 21
 Noctuidae, 79, 161, 220
norica, *Marpesia*, 77
Nosema, 106
Nothomastix
 chromalis, 75
 klotsi (new comb.), 76
 obliquifascialis (new comb.), 76
 pronaxalis (new comb.), 76
 pyranthes (new comb.), 76
 sisyroptila (new comb.), 76
 Notodontidae, 159

- Nymphalidae, 24, 44, 77, 87, 97, 110, 120, 235, 273, 302
 Nymphulinae, 75
- obliquifascialis*, *Nothomastix* (new combination), 76
- Ochlodes
batesi (new combination), 21
snowi (transferred to *Paratrytone*), 21
- Oeneis chryxus*, 110
- Oidaematophorus*
balanotes, 195
glenni, 197
grandis, 197
kellicotti, 197
lacteodactylus, 197
- Old World, 280
- Oligostigma bilinealis*, 76
- opaca*, *Liptena*, 208
- Opisthedeicta*, 76
- Opotegidae, 70
- Opotegoides scioterma*, 70
- Oregon, 70
- Oriental Region, 298, 301
- orientis*, *Bebearia*, 64
- orientis insularis*, *Bebearia*, 64
- orithya*, *Precis*, 88
- Ornipholidotos kirbyi*, 207
- Orsotriaena medus*, 87
- otis lysizone*, *Zizina*, 88
- overwintering, 97
- Pachliopta aristolochiae*, 86
- Palmer, W. A., 195
- palmira*, *Eurema dairia*, 124
- palatability, 77
- paludicola*, *Bebearia* (= *guineensis*, new syn.), 63
- Panoquina sylvicola*, 126
- Paradulcedo*** *mimica*, 44
- Papilio***
crephontes ab. "maxwelli", 238
homerus, 233
memnon, 86
- Papilionidae, 86, 125, 145, 233
- Parapoynx*, 76
- parasitoids, 197, 201, 233
- Paratrytone*, 6
aphractoia, 21
argentea, 21 (removed from *Paratrytone*)
barroni, 21 (removed from *Paratrytone*)
batesi, 21 (transferred to *Ochlodes*)
decepta, 21
melane, 12, 21 (transferred to *Poanes*)
monticola, 21 (transferred to *Poanes*)
polyclea, 21
rhaxenor, 21
snowi, 21 (new combination)
ulphila, 21 (transferred to *Poanes*)
- Pardomima***, 75
- Parnara* cf. *guttatus*, 89
- pathogen, 106
- pebrine, 106
- Peigler, Richard S., 167, 246, 313
- Pelopidas conjunctus*, 88
- Pentila***
bitje, 206
nigeriana, 204
picena cydaria, 206
- Peru, 73
- Petr, Daniel, 110
- phaon*, *Phyciodes*, 122
- phenology, 138
- Phoebis sennae*, 124
- Phyciodes phaon*, 122
- Phycitinae, 39
- phyleus*, *Hylephila*, 126
- picena cydaria*, *Pentila*, 206
- piera piera*, *Haetera*, 50
- piera ecuadora*, *Haetera*, 50
- Pierella*, 44
- Pieridae, 87, 124
- Pinheiro, C. E. G., 77
- plexippus*, *Danaus*, 97, 120
- Poanes*, 1
azin, 17, 21
capta, 19, 21 (new combination)
hobomok, 14, 21
inimica, 20, 21
lupulina, 20, 21
macneilli, 17, 21
melane, 12, 21
monticola, 19, 21 (new combination)
niveolimbus, 19, 21 (new combination)
psaumis, 1
taxiles, 14, 21
ulphila, 19, 21 (new combination)
zabulon, 14, 21
- Pococera* complex, 280
- poeyi*, *Appias drusilla*, 124
- polyclea*, *Paratrytone*, 21
- pomona*, *Catopsilia*, 87
- Polytremis lubricans*, 88
- Potanthus confucius*, 88
- Powell, Jerry A., 311
- prchali***, *Coloradia*, 128
- Precis*
amana javana, 87
atlites, 87
orithya, 88
- predators, 77, 138
- pronaxalis*, *Nothomastix* (new combination), 76

- proteus domingo*, Urbanus, 125
proteus santiago, Urbanus, 125
Protoleuron rhodogaster, 73
psaumis, Poanes, 1
pseudocentaurus, *Arhopala*, 88
Pseudohaetera hypaesia, 44, 50
Pterophoridae, 195
Ptelina carnuta, 204
Pyralidae, 39, 280
pyranthes, *Nothomastix* (new combination), 76
Pyraustinae, 75, 159
pyritosa, *Cithaerias*, 50
Pyrroglyra neaerea arge, 77

ramsdeni, *Heliconius charitonia*, 122
rearing, 160
Ribes hurtellum, 70
Rindge, Frederick H., 166
Robbins, Robert K., 298
rhaxenor, *Paratrytone*, 21
Rhizophora stylosa, 174
rhodogaster, *Protoleuron*, 73
rhombifolia, *Sida*, 24
rica, *Halotus*, 188
rodora, *Lacinioplia*, 79
rolla (ex *Poanes*), 3
Rosentiel, R. G., 70
rothi, *Telipna*, 206
Ruszczyk, Alexandre, 255
Rutowski, Ronald L., 24, 305

Salbia lauralis, 76
santiago, Urbanus *proteus*, 125
sappho, *Catocala*, 161
sarpedon, *Graphium*, 86
Saturniidae, 106, 128
Satyrinae, 44, 110
scioterma, *Opostegoides*, 70
seasonal variation, 106
senegalensis, *Bebearia*, 59
senegalensis katera, *Bebearia*, 60
sennae, *Phoebis*, 124
septentrionis, *Tirumala*, 87
Sesiidae, 265
Sesiinae, 265
sex attractant, 000
sexual selection, 24
Shaffer, Jay C., 39
Shields, Oakley, 235
Sida rhombifolia, 24
similis, *Liptena*, 208
Simon & Schuster's *Guide to Butterflies and Moths* (book review), 242
sisyroptila, *Nothomastix* (new comb., new syn. = *chromalis*), 76
Slotten, Jeffrey R., 161

Smith, Michael J., 128
snowi, *Paratrytone*, 21
Solis, M. Alma, 280
Sonora, 128
Sonoran Lepidoptera Survey, 128
sordida, *Lycomorphodes*, 160
Sphingidae, 73
Spizella passerina, 70
Stehr, Frederick W., 165
Steinhauser, Stephen R., 119
Stericta, 280
stigma, 182
Stolidoptera, 73
strabo, *Catochrysops*, 88
Strymon
 melinus, cover issue 1
 martialis, 124
 acis gossei, 124
stylosa, *Rhizophora*, 174
succession, 83
sylvicola, *Panoquina*, 126
symethus, *Miletus*, 88
Synanthedon canadensis, 265
systematics, 1, 39, 54, 73, 128, 182, 220

tagal, *Ceritops*, 174
tailori, *Heraclides andraemon*, 125
taminatus, *Hasora*, 89
tasar silkworm, 106
taxiles, *Poanes*, 14, 21
taxonomy, 1, 39, 54, 73, 128, 182, 196, 220
Telfer, William H., 169
Telicota augias, 89
Telipna rothi, 206
Temenis laothoe, 77
territoriality, 24, 110
Tetrarhanis diversa, 209
Texas, 160, 195, 265
The Common Names of North American Butterflies (book review), 310
The Development and Evolution of Butterfly Wing Patterns (book review), 305
The Nepticulidae and Opostegidae (Lepidoptera) of North West Europe (book review), 240

theognis, *Bebearia*, 61
theonus, *Leptotes cassius*, 124
thermal ecology, 97
thermoregulation, 97
Thornton, I. W. B., 83
Tirumala septentrionis, 87
Tortricidae, 269
transcontinental, 269
tripunctus, *Cymaenes*, 226
Troides helena, 87
Turner, Jon D., 215

Turner, T., 273
 type-localities, 18, 40, 54, 220
 Tyrannidae, 77
Tyrannus melanocholicus, 77

ulalume, *Catocala*, 161
ulphila, *Poanes*, 19, 21
 United States, 79, 159, 160, 220
 urban butterflies, 255
 urban ecology, 255
 urban Lepidoptera, 255
Urbanus
 proteus domingo, 125
 proteus santiago, 125
Urtica dioica, 303
urticae, *Aglais*, 302

Vanessa
 cardui, 235
 kershawi, 235
 Vane-Wright R. I., 273
vanillae insularis, *Agraulis*, 120

variation, 128
 velocimeter, 215
 Venedictoff, Nadia R., 73
verecunda, *Carmenta*, 265
verecundalis, *Ceratoclasia*, 76
 vicariance, 273
vicina, *Lacinipolia*, 80
 vulcanism, 83

 Wagner, David L., 314
 White, Raymond D., 310
 Williams, Carroll Milton (obituary), 169
 wing venation, 45
 Winter, William D., 307

zabulon, *Poanes*, 14, 21
Zizina otis lysizone, 88
Zizula hylax, 88
zoe, *Dryas iulia*, 119
zonalis, *Junonica evarete*, 122
 Zygaenidae, 160





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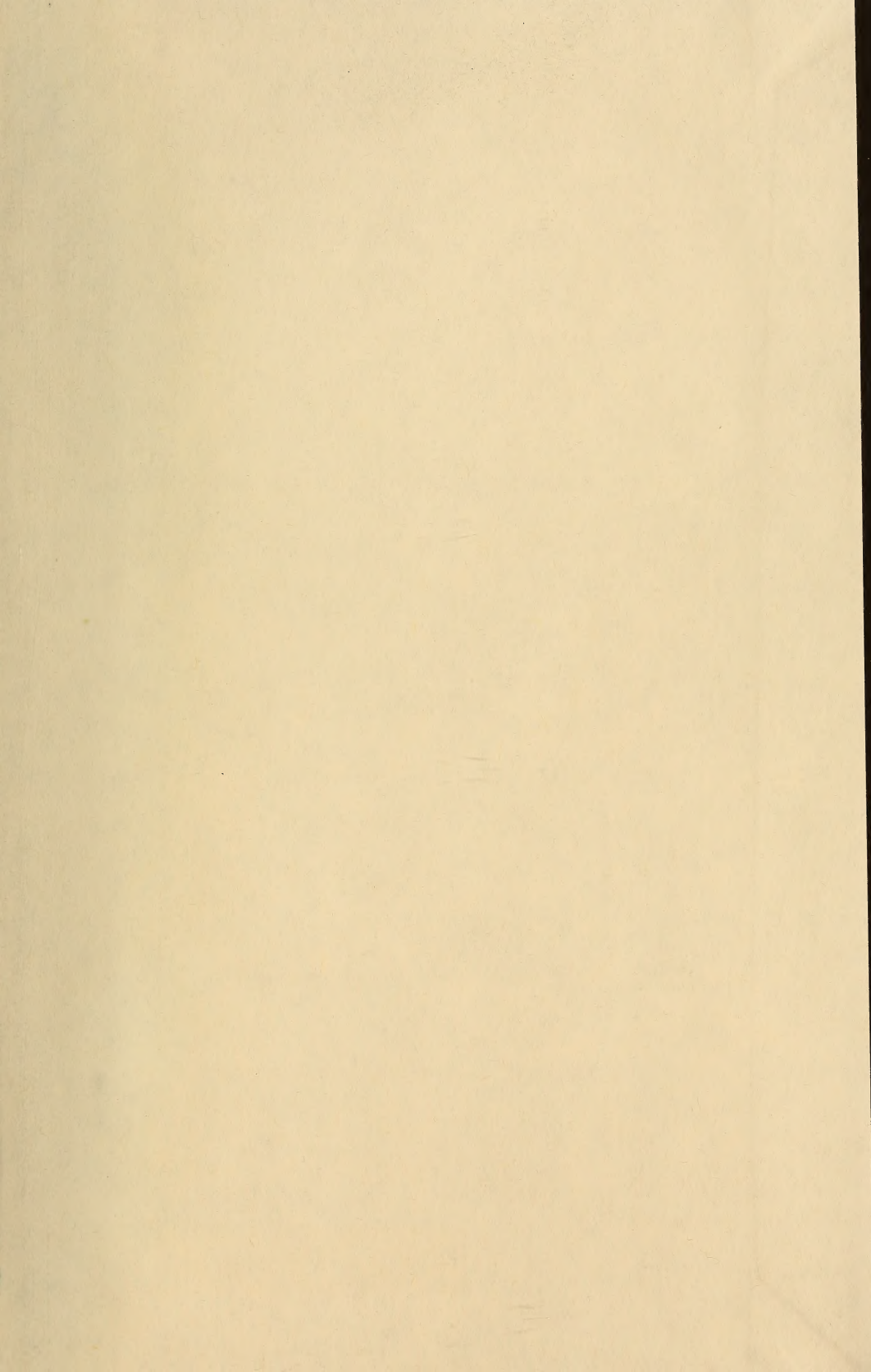
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CONTENTS

GRADIENTS IN BUTTERFLY SPECIES DIVERSITY IN AN URBAN AREA IN BRAZIL. <i>Alexandre Ruszczyk and Aldo Mellender de Araujo</i>	255
A NEW TEXAS CLEARWING MOTH (SESIIDAE: SESIINAE). <i>Thomas D. Eichlin</i>	265
HOLARCTIC DISTRIBUTION OF <i>CHORISTONEURA ALBANIANA</i> (WALKER), WITH NEW SYNONYMY (TORTRICIDAE). <i>P. T. Dang</i>	269
ANETIA JAEGERI, DANAUS CLEOPHILE AND LYCOREA CLEOBAEA FROM JAMAICA (NYMPHALIDAE: DANAINAE). <i>R. I. Vane- Wright, P. R. Ackery and T. Turner</i>	273
CHECK LIST OF THE OLD WORLD EPIPASCHIINAE AND THE RE- LATED NEW WORLD GENERA <i>MACALLA</i> AND <i>EPIPASCHIA</i> (PYRALIDAE). <i>M. Alma Solis</i>	280
TECHNICAL COMMENTS	
Comparison of butterfly diversity in the Neotropical and Oriental regions. <i>Robert K. Robbins</i>	298
Response to "Comparison of butterfly diversity in the Neotropical and Oriental regions" by Robert K. Robbins. <i>John B. Heppner</i>	301
GENERAL NOTE	
<i>Aglais urticae</i> (Nymphalidae): A nascent population in North America. <i>Jeffrey Glassberg</i>	302
BOOK REVIEWS	
The Development and Evolution of Butterfly Wing Patterns. <i>Ronald L. Ru- towski</i>	305
A Field Guide to Eastern Butterflies. <i>William D. Winter</i>	307
The Common Names of North American Butterflies. <i>Raymond R. White</i>	310
Moths of Australia. <i>J. A. Powell</i>	311
Moths of Australia. <i>Richard S. Peigler</i>	313
OBITUARIES	
Alexander Barrett Klots. <i>David L. Wagner</i>	314
Charles Gordon Campbell Dickson. <i>Stephen Frank Henning</i>	325
FEATURE PHOTOGRAPH	
Attracting and photographing <i>Agrias amydon</i> (Nymphalidae) in Brazil. <i>George O. Krizek</i>	334
INDEX TO VOLUME 46	336

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